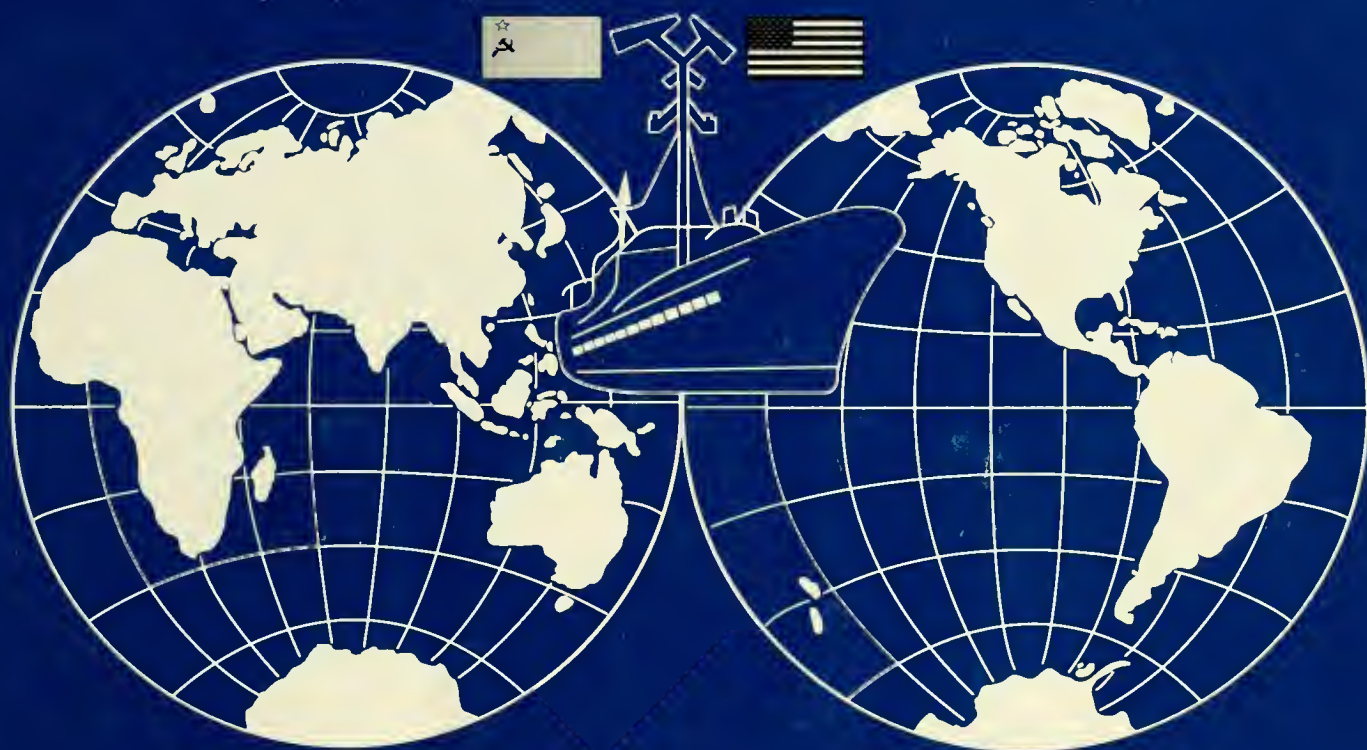
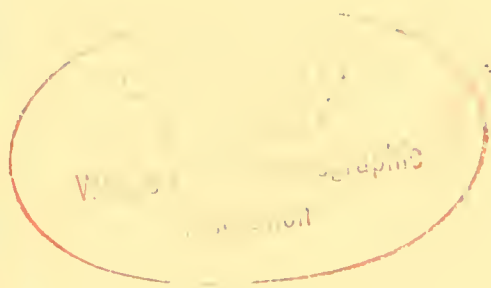


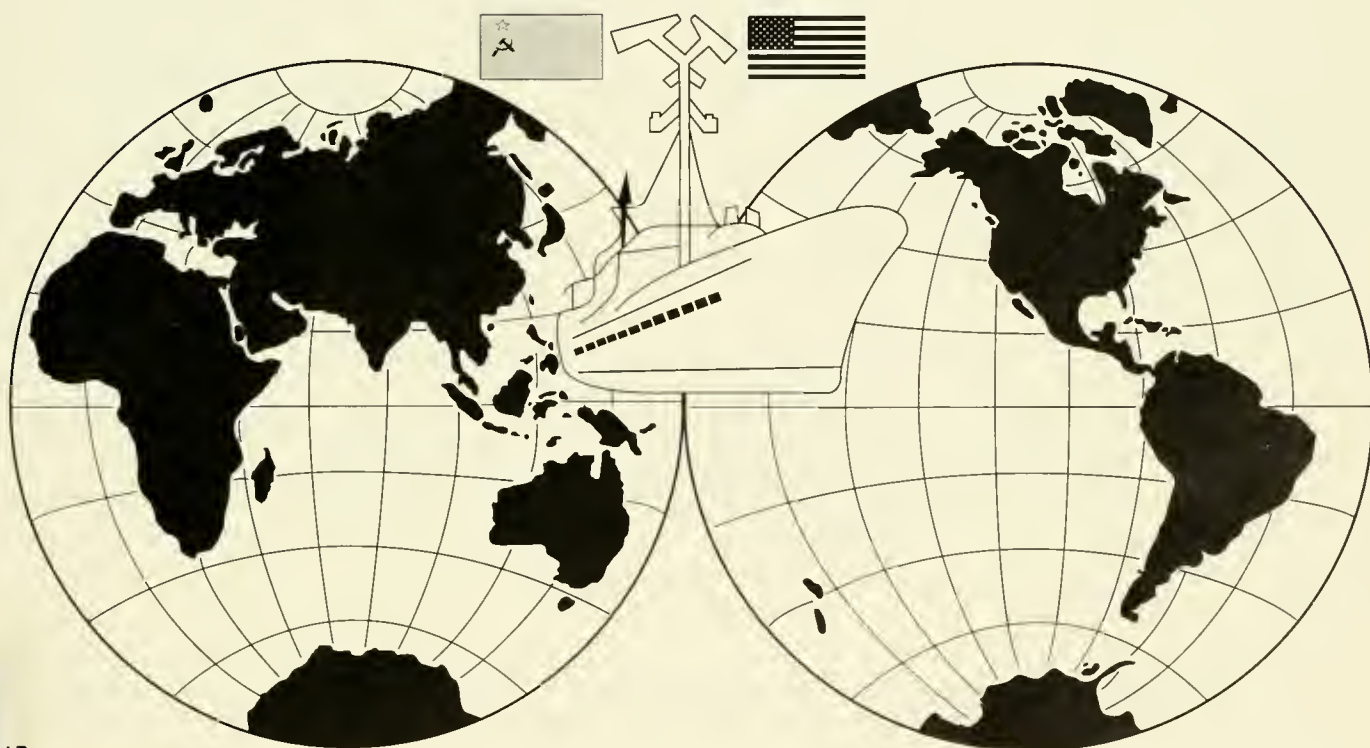
RESULTS OF THE FIRST JOINT US—USSR CENTRAL PACIFIC EXPEDITION (BERPAC)



AUTUMN 1988

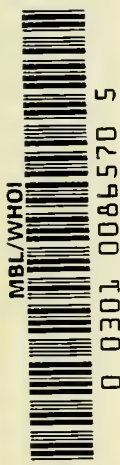


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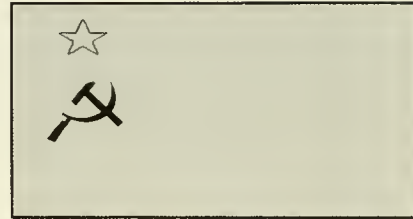


**Results of the First Joint
US–USSR Central Pacific Expedition
(BERPAC)**

Autum 1988



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Foreword

Included here in its entirety is the BERPAC Program paper, published in 1991 [J.F. Turner, H.J. O'Connor, Yu.A. Izrael, and A.V. Tsyban (eds.) (1991)]: BERPAC—A Program for Long-term Ecological Research of Ecosystems of the Bering and Chukchi Seas and the Pacific Ocean. National Fund for the Patuxent Wildlife Research Center, Bowie, Maryland]. BERPAC refers to joint research of the US and USSR in the Bering Sea and central Pacific Ocean since 1977. The Bering Sea portion of the project has included three joint research expeditions (1977, 1984, and 1988) between the two countries. The central Pacific portion of the project was established in 1988 when the first joint expedition took place. The central Pacific segment, therefore, has not had the opportunity to go through the same maturing process as that of the Bering Sea. As time goes on, and research continues, goals and objectives to be accomplished will be further developed. The paper is included here as a Foreword to show the correlation with this volume's sister monograph, Results of the Third Joint US-USSR Bering & Chukchi Seas Expedition (BERPAC), Summer 1988.

BERPAC

A Program for Long-term Ecological Research of Ecosystems of the Bering and Chukchi Seas and the Pacific Ocean

Introduction

Deterioration of ecosystems on a large scale threatens many functional equilibria in the biosphere. This problem is particularly urgent for the World Ocean, which is the sink for many different pollutants that can produce significant ecological impacts.

The ocean is able to assimilate a certain amount of anthropogenic compounds due to "self-purification" without visible deterioration of the ecosystem. However, continuous increase in the flux of pollutants to the ocean creates the need for study of the resistance of marine ecosystems to anthropogenic impacts. Investigations of ecological consequences and elucidation of causal relationships between the impact levels and adverse biological effects are only poorly understood for the marine environment. The study of these interactions and responses is interdisciplinary in character and covers different fields of biology, ecology, chemistry, and physics of the sea.

The dynamics of marine ecosystems, including biological and physical processes and biogeochemical cycles, are closely related to changes in the climate of the Earth. The predicted global warming may have a pronounced effect on certain vital processes in the World Ocean, especially the resistance of its ecosystems to anthropogenic contamination. This is because the living ocean determines, to a great degree, the normal functions of the Earth's climatic system.

Long-term observations of physical, geochemical, and hydrobiological processes are necessary for the assessment of ecological consequences of contamination in the ocean environment and isolation of local anthropogenic effects compared to the effect of climatic variability.

The Bering Sea is located between the coasts of the Soviet Far East (USSR) and Alaska (USA), and naturally an interest in the study of its ecosystems has been shown by Soviet and American scientists (Izrael & Tsyban, 1983a, 1977, 1990; Roscigno, 1990).

In spite of comprehensive studies carried out in the Bering Sea in the last few years (Izrael *et al.*, 1988b; Izrael & Tsyban, 1989, 1990; Coachman, 1990; Roscigno, 1990), a number of the oceanographic, hydrochemical, and biological parameters

determining its ecosystem functions are as yet poorly known when compared with, for instance, the Baltic, Mediterranean, and Black Seas. For example, the joint bilateral program of Bering/Chukchi investigations have been carried out for more than 13 years with the production of three monographs of cruise results. However, the as yet inadequate data on the characteristics and processes occurring in the ecosystems of the Bering Sea and North Pacific waters has led to the organization and implementation of an international program: Long-term Ecological Research of Ecosystems of the Bering and Chukchi Seas and the Pacific Ocean (BERPAC Program).

Goals, Objectives, and Scientific Basis of the BERPAC Program

Goals

The goal of the BERPAC Program is to examine the status of marine ecosystems of the Pacific Ocean, Bering Sea, and Chukchi Sea and to assess their role in determining global climate. BERPAC will study the dynamics of these ecosystems related to conditions of global climate change and anthropogenic contamination.

Objectives and Scientific Basis of the BERPAC Program

Objectives of the BERPAC Program consist of the study of the biogeochemical cycles of contaminants, related oceanographic processes, and food-web interactions in the North Pacific waters that flow through the Bering/Chukchi Seas, including study of the behavior of organic pollutants at the water/sediment interface, since sediments are sources of the secondary pollution of ecosystems. Important topics of study are the control and the accumulation of pollutants in bottom deposits, and the study of their migration within the sediments and exchange with overlying waters are important topics of study.

1. Assessment of Ecological Consequences of Contamination

Progressively severe changes in chemical contamination of the ocean biosphere are on the increase. Anthropogenic

impacts influence not only the biotic component of the marine environment but different abiotic components as well. Such impacts lead to even more significant changes in the World Ocean and in the biosphere as a whole.

Specific features of the Bering Sea and other ecosystems with "background" levels of contamination are such that they are especially vulnerable because of the continual input of small doses of pollution. This leads to a gradual accumulation of pollutants, and may ultimately cause the degradation of the ecosystems. Therefore, ecological investigations and monitoring of the background regions of the ocean, especially in such highly bioproduktive zones as the Bering Sea, are of great importance. In order to assess the ecological consequences of the pollution and isolate anthropogenic effects from the background of natural variability, it is necessary to make long-term observations of fundamental physical, chemical and biological processes in selected areas of the above regions. These regions differ in their geographical location, as well as in the subsystems of their ecosystems, and are subjected to different anthropogenic impacts.

2. Study of the Processes Determining the Assimilative Capacity for Contaminants in Marine Ecosystems

In the marine environment, various physical, chemical, and biological processes occur through which contaminants can be eliminated from the ecosystem without serious disturbances of the biogeochemical cycles of the elements or changes in the biota. Diverse oceanological investigations carried out in the last few years have shown that the biotic component is important in the fluxes of pollutants.

The ability of an ecosystem to protect itself against a foreign interference at the expense of many biological, physical, and chemical processes is its natural "immunity" and the measure of this immunity is its assimilative capacity.

According to the contemporary interpretation (Izrael & Tsyban, 1983b, 1989; Izrael *et al.*, 1988b,c), the assimilative capacity of a marine ecosystem is an integral function of its existing environmental status that reflects the ability of physical, chemical, and biological processes for elimination of pollutants and their impacts on the biota.

When using the concept of assimilative capacity in practice, it is necessary to bear in mind that a marine ecosystem occupies a finite volume that may be isolated on the basis of the spatial distribution of organisms of various trophic levels, groups of ecologically similar species, and production/destruction processes, as well as physical and chemical characteristics. Hence, the assimilative capacity of each specific ecosystem also has a value that objectively characterizes existing properties of the marine environment. This value could be determined in practice on the basis of integrated investigations and monitoring of the marine environment, carried out in accordance with existing methodological recommendations (Izrael & Tsyban, 1983b, 1985, 1987, 1989; Izrael *et al.*, 1988b).

The use of this concept in the BERPAC studies will include investigations of the following basic problems: 1. quantitative assessment of the balance of chemical elements in the ecosystem and possible changes in residence times due to disturbances; 2. assessment of adverse biological effects at

the level of population and communities; and 3. determination of the critical concentrations at which contaminants adversely impact the marine organisms and communities.

Thus, a conceptual model of the assimilative capacity, based on a better understanding of the laws of marine ecosystem functions, can serve as a theoretical basis for the development of forecasts of both the immediate and long-range consequences of anthropogenic and climatic impacts on the ocean ecosystems.

3. Study of the Elements of the Biogeochemical Carbon Cycle and Its Role in Global Climatic Processes

Global warming predicted in connection with the developing greenhouse effect depends directly upon the biogeochemical cycle of carbon—the most important process forming the Earth's climate. The basic elements of this cycle are carbon-dioxide and other "greenhouse gases" exchanged within the ocean-atmosphere system, the function of the carbonate system, and the turnover of organic forms of carbon in the ocean.

The most intensive uptake of atmospheric CO₂ occurs at high latitudes, as a result of favorable thermal and hydrological conditions (low sea surface temperature and permanent downwelling) in the region. These peculiarities explain the important role of the Bering Sea, a subarctic body of water having a large area, in the global cycle of carbon dioxide.

The relationship between the rates and directions of CO₂ flow within the ocean-atmosphere system directly affects the functioning of the carbonate system. So, in the conditions where global warming is induced by an increase in the concentration of atmospheric CO₂, a shift of the equilibrium between carbonate forms of carbon in seawater might occur, which will be accompanied by a decrease of pH and, consequently, elevation of the lysocline.

Investigations of these processes, directly affecting the sedimentation of organic carbon and the vital functions of marine organisms, are only possible with direct determination of all components of the carbonate system (i.e., HCO₃⁻, CO₃²⁻, H₂CO₃, and CO₂).

To fully understand all of the characteristics of the oceanic portion of the global carbon cycle, it is necessary to study the processes of the circulation of its organic forms in the composition of dissolved and particulate matter and in the cells of living organisms (Zaitsev, 1970, 1980, 1985).

The dynamic equilibrium of dissolved and particulate organic matter, living matter, and the content of organic carbon within water masses depends on the relations between production/destruction processes established in the ecosystem. In this connection, the predicted effects of global warming on the bioproduktivity of the Bering Sea ecosystem will influence the organic carbon cycle. In order to study possible changes, long-term observations of the concentrations of all organic forms of carbon are necessary.

Thus, to establish the carbon balance in the Bering Sea ecosystem, comprehensive long-term observations of all carbon constituents in the aquatic interface and the study of quantitative and qualitative composition of both the carbonate system and organic forms of carbon are required.

4. Investigation of the Physical Mechanisms Related to Climate Variations

Existing global physical models of the ocean–atmosphere system do not make it possible to predict possible climate changes on a regional scale because of the extreme complexity of the modeled systems. Additional investigations of the physical development of regional models, in particular of a model for the Bering Sea, are an important need for long-term climate forecasting at the present time.

This problem could be solved on the basis of long-term oceanological observations in different regions of the Bering Sea, which are aimed at the acquisition of systematic information on the vertical distribution of temperature, heat content of the active layer and its variability with time, the structure and variability of ocean circulation, heat transfer by the basic sea currents, and heat and moisture fluxes across the sea surface.

To develop the above models it is necessary to know the regularity of water mass formation in the deep basins of the Bering Sea. The following issues are not yet clear: North Pacific water must be involved in bottom water formation, but given the topographic isolation of Bowers and the central basins, how and where does this take place? Are sources the same for the different basins? What are the flushing rates (e.g., residence times)?

There are three hypothetical mechanisms by which bottom water might possibly be formed: 1. modification of surface (upper layer) water within the confines of the sea by cooling and brine enhancement through ice formation, creating water sufficiently dense to sink to the bottom; 2. subsurface mixings of North Pacific water with appropriate Bering Sea waters as it crosses the sills in the Aleutian–Komandorskiy Island arc passages; and 3. direct advection of deep North Pacific water in through Kamchatka Strait and then sequentially through the gaps into the other basins.

The BERPAC Program will investigate the mechanism of deep water formation, renewal rates, and flushing of the basins.

Area of Investigations

While selecting the study areas and location of stations in the Bering Sea, the diversity and contrast of ecological conditions in different regions of the sea were taken into account.

In order to reflect a variety of ecological conditions in the Bering Sea more completely, it seems appropriate that integrated expeditions include work on polygons located in different areas of the sea (with the purpose of obtaining representative data on the structure and functions of the basic marine ecosystems) and work across transects (with the purpose of determining the space and time variations of the key ecological parameters).

Investigations within the framework of BERPAC will be conducted on four polygons where investigations were carried out in 1981 (during the integrated ecological expedition aboard the research vessel (R/V) *Akademik Shirshov*) and in 1984 and

1988 (during the second and third Soviet–American ecological expeditions aboard the R/V *Akademik Korolev*) (Izrael & Tsyban, 1987, 1990; Izrael *et al.*, 1988a; Roscigno, 1990).

Deep stations will be repeated at four centered polygons in the four deep basins. The center station of each polygon will also be a location for a mooring containing sediment traps and current meters, funding permitting. Four other mooring locations will cover the entrance from the North Pacific (in the deep channel northwest of Komandorskiy Island), the main gaps in the ridges north of Attu, and a location on the east side of the Central Basin under the Bering Slope Current. The mooring locations are also deep oceanographic stations, and 11 additional stations will provide continuity among the deep waters.

In addition to polygons, observations are planned at stations along the transects located in areas that are not yet completely understood, such as the Gulf of Anadyr, the Chirikov Basin, the Gulf of Alaska, the northern portion of the Pacific Ocean, and the deep-water central and southwestern areas of the sea. Larger scale studies in the Chukchi Sea and central Pacific ecosystems are also planned. The program for individual expeditions will be discussed specifically during joint symposia.

Proposed Observations

Complex observations during the ecological expeditions include meteorological (including aerological and geophysical studies), oceanographical, and ecological observations. Specifically, the following observations will be made:

A. Meteorological observations will include routine observations of meteorological parameters, such as studies of direct solar radiation intensity and ultraviolet irradiation, cloud and cloud type studies, and collection of samples of atmospheric precipitation for chemical analyses. Aerological and geophysical observations will include temperature and wind sounding with the aid of radiosondes. Air samples will be collected for determination of sulfates and nitrogen oxides. Visual observations of oil and oil product contamination on the sea surface will be recorded.

B. Oceanographic observations at designated sampling depths in the water column will include temperature, salinity, nutrients, oxygen content, water color and transparency, biogenic elements, alkalinity, and petroleum hydrocarbons. Tracers for water mass types will include stable isotope content of seawater (oxygen, deuterium, tritium, freons, silica, and carbon 14). In addition, current velocity and direction will be determined, and sediment trap collections will be made.

C. Ecological observations will include studies of the atmosphere, sea surface microlayer, water column, and bottom deposits in the environment.

1. Atmosphere

In rainfall, pH and the content of organic contaminants will be determined. In dust particles, the content of organic contaminants and metals will be determined. In the air at the

sea surface, the content of “greenhouse” gases (CO₂, nitrogen oxides), oxygen, and chlorinated hydrocarbons will be determined.

2. Sea surface microlayer, water column, and bottom deposits

Water samples will be collected in the surface microlayer and at standard hydrological depths and at selected experimental depths (e.g., thermocline, pycnoline, phyto- and zooplankton maxima and sediment–water interface) (Zaitsev, 1980).

a. In the surface microlayer, the following elements and parameters will be determined:

- organic carbon;
- contaminants (toxic metals, and aliphatic aromatic and chlorinated hydrocarbons), the state of neustonic communities; determination of the structural characteristics of bacterioplankton; total numbers, biomass of microorganisms, most probable numbers (MPN) of indicator groups of bacteria (e.g., paraffin-oxidizers, PCB-transforming and neurotrophic saprophyte groups), and indices of phyto- and zooneuston (numbers, biomass, species, size composition, species mass and indicator forms), mutation (teratogenesis) of zooneuston organisms.

b. In the water column, the following parameters will be determined:

- water optical indices;
- contaminants (toxic metals, and aromatic, aliphatic and chlorinated hydrocarbons);
- the total concentrations of organic carbon and its composition;
- elements of the carbonate system (CO₃, HCO₃, CO₂);
- characteristics of bacterioplankton (total numbers, biomass, MPN, and distribution of indicator groups); and their biochemical and genetic capacities;
- structural characteristics of phyto-, microzoo-, and mesozooplankton (numbers, biomass, size, and species composition, species mass, and indicator forms);
- functional characteristics of planktonic communities (heterotrophic CO₂ assimilation by bacteria, bacterial production, phytoplankton productivity); and
- biosedimentation rate of particulate matter.

c. In the biota, the following parameters will be determined:

- contaminants (toxic metals, and aromatic, chlorinated and aliphatic hydrocarbons); and
- organic carbon content, stable carbon, and nitrogen isotope content.

d. In bottom sediments, the following elements will be determined:

- determinants (toxic metals, and aromatic, chlorinated and aliphatic hydrocarbons);
- total organic carbon and nitrogen;
- stable carbon and nitrogen isotopes; and

- structural characteristics of zoobenthos (numbers, biomass, species composition, and species mass).

3. Higher trophic levels

During the expedition, zoological observations will be carried out: numbers, distribution, and migratory patterns of fish, birds, and marine mammals.

4. Model experiments

Model experiments will be performed under conditions similar to natural situations. During these experiments, the following parameters will be studied:

- photochemical oxidation of organic contaminants;
- biodegradation potential of bacterioplankton with respect to organic contaminants (benzo(a)pyrene, PCB, etc.);
- combined influence of contaminants on biological “targets” and establishment of “critical” concentrations of the impact on plankton communities in the conditions of controlled ecosystems (Izrael *et al.*, 1988a); and
- sediment respiration and nutrient flux experiments.

Connection with Other International Programs

The BERPAC Program has much in common with other international programs, but at the same time it has its own particular features mentioned earlier. Wide cooperation with other similar international projects is built within the framework of this program—in particular, in the preparation of joint marine expeditions. Wide data exchange is also planned.

Schedule of Activities and Applications of Results

Since 1977, successful joint investigations of Soviet and American scientists have been carried out in the Bering Sea within the framework of the specific theme of the bilateral cooperation “Bering Sea” (Project “Comprehensive Environmental Analysis;” Subproject “Comprehensive Analysis of Marine Ecosystem State and Ecological Problems of the World Ocean”). Important stages of this cooperation were three joint ecological Soviet–American expeditions in the Bering Sea on the R/V *Volna* (Summer 1977), R/V *Akademik Korolev* (Summer 1984 and 1988), and several symposia on the preparation of scientific programs and analyses of the results of these expeditions, as well as three monographs describing the results of long-term Soviet–American investigations in the Bering Sea (Izrael & Tsyban, 1990; Roscigno, 1990). It is expected that these expeditions will be every four years and followed by international symposia and joint publications.

Monographs on the results of future expeditions will be published. It is expected that seminars and symposia within the framework of the BERPAC Program will be conducted. Also included in the plans are special intercalibrations, a wide exchange of specialists, and joint experimental work.

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Protocol of the First Joint US–USSR Central Pacific Ocean Expedition on the R/V *Akademik Korolev*

In accordance with the memorandum of the 11th meeting of the US–USSR Joint Committee on the Environment Protection (Moscow, USSR, February 1988) and the recommendation of the “Soviet–American Conference on the Ecology of the Bering Sea” (Batumi, USSR, March 1988) and the plan of the joint bilateral activity of 02.07–2101, “Comprehensive Analysis of Marine Ecosystems and Ecological Problems of the World Ocean,” the Third Joint US–USSR Bering & Chukchi Seas Expedition was held on 26 July 1988 on board the Soviet research vessel *Akademik Korolev*. The second leg of this expedition was conducted from 9 September to 31 October in the central Pacific Ocean and South China Sea. The delegation was headed by Prof. Alla V. Tsyban and Dr. Gregory J. Smith. Nearly 10,000 nautical miles of ocean were covered during this leg of the expedition.

The Soviet delegates were represented by participants in the cruise from the USSR State Committee for Hydrometeorology and Control of Natural Environment; the Academy of Sciences from the USSR; and the Academies of Sciences from Ukraine, Belyorussia, and Estonia. A list of participants is given as Appendix A.

Six American delegates joined the expedition during the port of call in Hilo, Hawaii, on 9 September 1988 and were represented by participants from the US Fish and Wildlife Service (Department of the Interior), and the University of Washington. A list of participants is given as Appendix A.

The principal objective of the second leg of the Third Joint US–USSR Expedition was to conduct comprehensive studies of the ecology of the central Pacific Ocean with an emphasis on ecosystem processes and the effects of anthropogenic pollutants on those systems. Included in this research was a complete zoological, chemical, and microbiological assessment of an isolated tropical coral atoll, Caroline Atoll, Kiribati. Hydrological stations were included along the route from Hawaii to Christmas Island, where a port of call was made to bring aboard a wildlife biologist from the government of Kiribati for studies of Caroline Atoll. During the period of 22–29 September, extensive studies of this remote atoll’s ecology were conducted and an assessment of the atoll’s status with respect to environmental contamination was made. A complete survey of the atoll’s plant and bird communities was also done. A full ecological station was sampled offshore from the atoll and series of four more stations were included enroute to Ratawa where the Kiribati representative disembarked. After Tarawa, the research vessel proceeded to 11°N latitude. Along the 11° transect, six ecological stations were studied in the Marianas section. The first station was in more than 6,000 meters of water, the last station along this transect was near the eastern Philippines, and the *Akademik Korolev*

proceeded through the Straits of Mindanao into the Mindanao, Sulu, and South China Seas. This route avoided Typhoon Ruby, which was located in the north Philippines and caused a severe loss of life and property in that area. On 25 October 1988, a three-day anchor station began in the South China Sea at 6°N latitude, three miles west of the 107th parallel. This long-term ecological station was the first in a series of five as the expedition proceeded into Singapore. Arrival at Singapore was on 31 October 1988, completing the second leg of the joint American–Soviet expedition of 1988. The route of the expedition is shown in the Frontispiece.

The main scientific tasks:

1. Biological, chemical, and physical fundamental data were collected to provide a comprehensive ecological and oceanographic profile of the central Pacific Ocean and South China Sea. These data provided a basis for comparison with the Bering and Chukchi Seas.

2. Cooperative studies of the methodology of collection, quantification, and chemical analysis of plastic debris were conducted to assess the overall hazard of plastics to marine life.

3. The ecological health of a remote coral atoll in the central Pacific was determined. Complete studies of the bird and plant communities were done. Studies of chlorinated hydrocarbons, their concentrations, distribution, and degradation by photolytic and microbiological processes were determined, thereby providing an assessment of the effects of anthropogenic activities.

In accordance with specialties of the expedition’s participants, working groups were organized. At these meetings, work schedules, joint studies, and model experiments were planned. During the expedition, meetings of the Scientific Council Board were also held. Discussed at these meetings were the important scientific findings of the expedition, comparing the Pacific Ocean and the Bering and Chukchi Seas. Also discussed were new areas of investigation that were introduced into the research effort with the new delegation of American scientists on the second leg. These areas included studies of marine plastic pollution, bird ecology, and the collection of biota for radionuclide analysis. Cooperative studies of the degradation and photolytic products of benzo(a)pyrene were expanding during this leg of the expedition.

Complex ecological studies were undertaken for the first time in the equatorial part of the Pacific Ocean. Unique joint studies that were undertaken to study the ecosystem of Caroline Atoll, an extremely remote area removed from the main sources of anthropogenic influences, are especially interesting. During the course of the cruise, results of preliminary investigations were obtained.

The concentration of dissolved oxygen in the lagoon waters of Caroline Atoll reached 115 to 126%, and the vertical distribution of hydrochemical parameters were relatively homogeneous. Salinity in lagoon waters was slightly higher than in water sampled outside of the lagoon (ocean water); the average values for lagoon and adjacent ocean water were 36.05 and 35.85 parts per thousand, respectively. Nutrient concentrations were lower in lagoon water than in coastal water: silicon and phosphorus were two times lower, nitrates were one and one-half times lower. According to studies of hydrooptical characteristics the lagoon waters do not differ significantly from the ocean waters.

The mean rate of biosedimentation of particulate organic matter (POM) in the water column from 0 to 100 m in the area investigated in the tropical zone of the Pacific Ocean was found to be 14.2 to 72.5 mg of dry matter/m³/day. In coastal waters of the atoll this rate was 64.5 mg dry matter/m³/day. The rate of biosedimentation in the surface water was two times higher than the rate at a depth of 100 m.

The most probable number (MPN) of heterotrophic saprophytic bacteria in the water inside and outside of the Caroline Atoll lagoon was 1,000 to 10,000 cells/ml. The MPN of paraffin-oxidizing, benzo(a)pyrene-transforming, and PCB-transforming bacteria in the water near the atoll was 10 to 1,000 cells/ml. In the water inside of the lagoon the MPN of microorganisms of these groups was less: 3 to 10 cells/ml. This information gives us the ability to characterize the atoll's water as clean, without anthropogenic pollutants.

The dominant pollutant in the atoll's ecosystem, in the widely investigated range of chlorinated hydrocarbons, was DDT and its metabolites (approaching 1 ng/l). Other substances observed in the pollutant benzo(a)pyrene were more intensive at Caroline Atoll than in the tropical zone of the ocean. In one hour, the amount of benzo(a)pyrene destroyed approached 85%, and after three hours more than 95% of experimentally added benzo(a)pyrene was destroyed. Ecotoxicity experiments conducted *in situ* dealing with the influence of benzo(a)pyrene, PCB's, copper, and cadmium on planktonic communities of the atoll's waters showed higher vulnerability of planktonic organisms to toxic metals and were relatively more resistant to benzo(a)pyrene and PCB's in comparison with the northern seas.

The distinctive feature of the zooneuston of the Caroline lagoon in comparison with the adjoining oceanic waters is the presence of a neuritic complex of organisms (larval stages of benthic animals and the early stages of Copepoda). The mean number of organisms was 64 ind/m³, 26 less than in the coastal waters of the atoll. Nevertheless, the zooneuston of the lagoon play an important role in the formation of the coastal water fauna.

A unique *Acropora-Tridacna* reef, dividing the lagoon, was discovered in the southern part of the atoll. Its length was more than one kilometer and its width was 15 to 20 m. At certain places along the reef, the *Tridacna* formed a dense aggregation with numbers approaching 40 ind/m².

More than 42,000 m² of Pacific Ocean surface water were sampled for plastic debris and macroscopic spherules. Plastics were recovered at six of the 29 different stations sampled.

At two of these stations, tar balls were also recovered. The density of surface plastics in areas that had positive samples ranged from 0.00782 to 0.19481 mg plastic/m². Because marine growth on the surface of plastics may alter the specific gravity of floating debris, sampling was also done at the thermocline to determine if plastic could be contaminating this important subsurface stratum. None of the 51,600 m³ of water sampled at the thermocline at nine different stations contained any plastics or anthropogenic materials. The surface water of the Caroline Atoll lagoon was sampled at two locations using a 102 neuston net. More than 21,500 m² of water sampled showed no evidence of plastics or other debris. Extensive sampling of surface and subsurface water was also done in the South China Sea. Although a wide variety of anthropogenic materials were recovered in surface tows, few plastic cylinders (raw material) were found. One sample from the thermocline contained plastic line, the most common form of plastic recovered in this area. Another surface sample from the South China Sea contained more than 164 tar balls greater than 4 mm in diameter.

Detailed data on the plants, seabirds, landbirds, mammals, reptiles, and human disturbance were obtained from 39 islets at Caroline Atoll. The flora consists of 19 species (one new to the island) organized into 4 natural and 4 anthropogenic plant communities; 92% of the islets are pristine. Eleven species of seabirds breed (red-tailed tropicbird is a new record); the sooty tern, with 189,000 breeding pairs, was the most abundant species. The long-tailed cuckoo was recorded for the first time in the Line Islands.

At-sea observations of marine birds indicated high densities near uninhabited islands and in known areas of high productivity. Low densities were observed in areas of low ocean productivity and in areas with high human disturbance (Gilbert Islands, and the Bohol, Sulu, and South China Seas).

Beach surveys for anthropogenic debris were done on nine islands of Caroline Atoll. Plastic and styrofoam objects accounted for 75 to 80% of the total number of items observed; however, glass bottles and fishing gear were significantly more important with respect to volume and biomass of debris. Observations were also made at sea to determine the amount of floating debris.

Samples were collected at Caroline Atoll and selected ocean sampling stations for radiological analyses. These analyses will compare natural versus anthropogenic radioisotopes. Radioisotope concentrations at Caroline Atoll will be compared to similar samples obtained in the Marshall Islands that contain contamination from atmospheric nuclear weapons testing 30 years ago.

At the end of the joint expedition on board the *Akademik Korolev*, there was an exchange of preliminary data. Future exchanges of data and results of analyses will occur in a series of three exchanges: 1. 1 March 1989; 2. 1 June 1989; and 3. 1 October 1989.

Both sides note with satisfaction the friendly and constructive atmosphere of the expedition's work and the effectiveness of joint observations allowing for a variety of oceanographic and ecological studies.

The American delegation wishes to extend their sincerest gratitude to the Soviet participants of the expedition. The science staff and ship's crew provided an atmosphere conducive not only to research but also the many friendships that resulted from our meeting. The American delegation would especially like to thank Professor A. V. Tsyban and

Captain O. A. Rostovtsev for the wealth of scientific and maritime knowledge provided the foundation for this highly successful scientific endeavor.

This protocol was written in English and Russian and was signed on board the research vessel *Akademik Korolev*, 1 November 1988. Both texts are equally authentic.

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(This text is a reproduction of the protocol written on board the R/V *Akademik Korolev* in 1988. The original was signed by both project leaders.)

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Without each participant of the expedition, and each author of research results, there would be no need for a monograph. There are far too many to name here; however, their names are listed with each subchapter and in Appendix A in this volume. It is their interest and excitement for the research presented here, and their spirit of cooperation so necessary for an international project, that provide the essence of the scientific accomplishments.

We are indebted to each of the US and USSR chapter editors for their help and their patience with the seemingly endless questions and tasks assigned to them, and last but certainly not least, for their sense of humor which is often the only saving grace in putting together a volume of this magnitude. Their names are listed alphabetically below:

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The “Production Team” at Patuxent Wildlife Research Center—**Kinard Boone, Patricia A. Holt, Susan A. Liga, Robert E. Munro, Patricia A. Nagel**, and **John C. Sauer**—deserves recognition for their dedication to meeting the challenge of producing a quality volume in time for it to be distributed to participants on the 1992 Expedition.

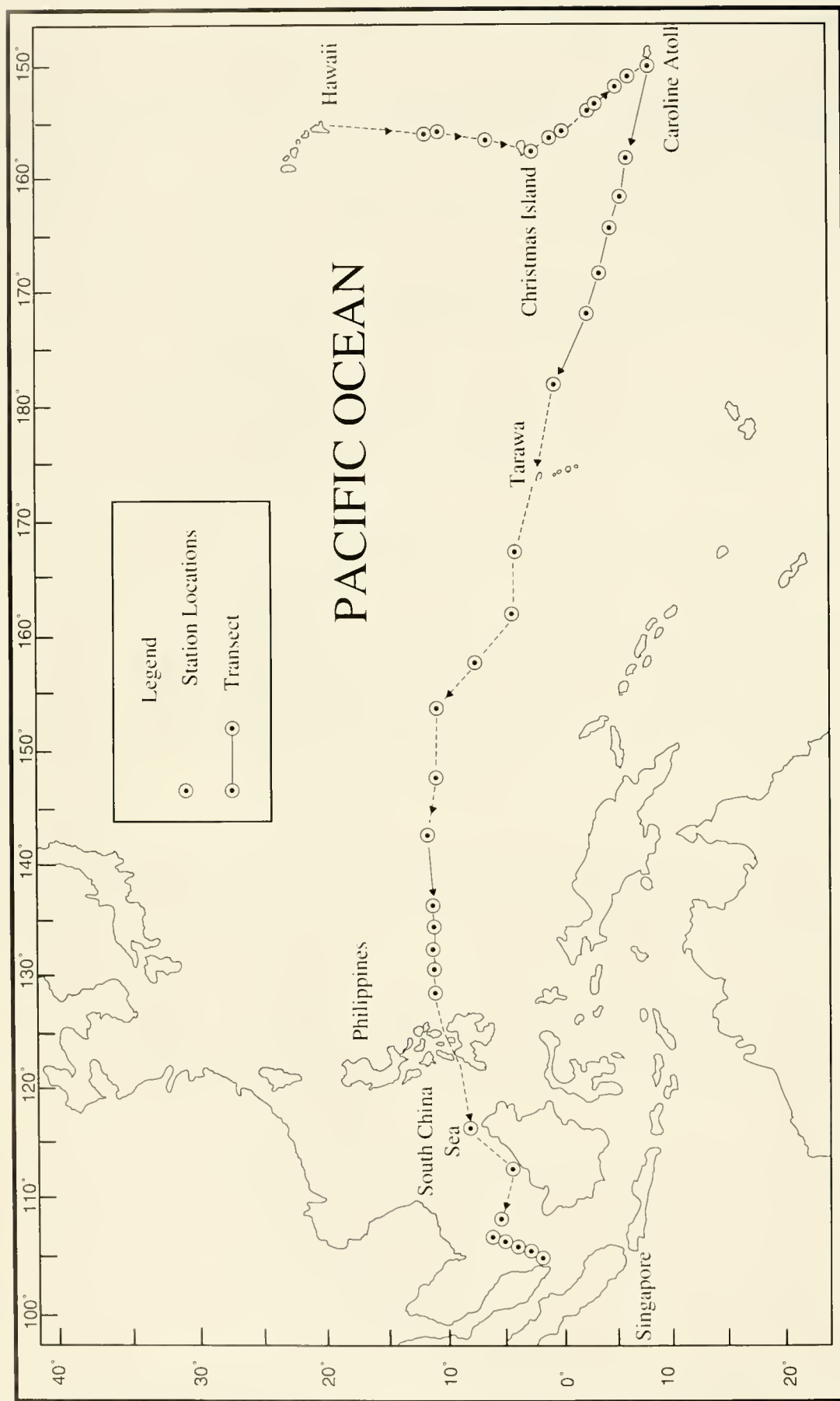
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Frontispiece. Cruise track of the First Joint US-USSR central Pacific Expedition (BERPAC), Autumn 1988, on board the Soviet research vessel *Akademik Korolev*.

Chapter 1:

ECOLOGICAL INVESTIGATION OF A CORAL ATOLL IN THE CENTRAL PACIFIC

Editor:

CAMERON B. KEPLER



CAROLINE ATOLL

0 1000 2000
METERS



Chapter 1 Frontispiece. Air-mosaic of Caroline Atoll, RNZAF 6569. Reproduced by permission of the Lands and Survey Department, New Zealand.

1.1 Ecological Studies of Caroline Atoll, Republic of Kiribati, South-central Pacific Ocean

Part 1. History, Physiography, Botany, and Islet Descriptions

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Introduction

On 26 July 1988, the Soviet research vessel *Akademik Korolev* sailed from Vladivostok enroute to Dutch Harbor, Alaska. There, Soviet oceanographers joined their American colleagues to investigate the Gulf of Alaska and the Chukchi Sea in the Third Joint US–USSR Pering & Chukchi Seas Expedition. When the arctic research was completed in early September, the ship headed toward the central Pacific. A rendezvous for a second contingent of Americans took place in Hilo, Hawaii, on 9 September. Six Americans joined the ship, which set sail on a cruise track of 14,892 km that terminated 6 weeks later in Singapore. An important part of the expedition was research in and around little-known Caroline Atoll, at the southeastern edge of the Line Group. On Christmas Island, we picked up Katino Teeb'aki, a conservation officer for the Republic of Kiribati, who represented his government and helped our land-based research efforts. After landing on Caroline on 22 September, we camped in 2 locations for 7 nights, surveying the terrestrial plants and animals on all 39 islets. Caroline is a remarkably pristine atoll with its native plant communities nearly intact on all but three islets, and teeming seabird communities that, collectively, are second in the Line Group only to Christmas Island (Kiribati) in diversity. For several historical reasons, the natural values of this spectacular blend of marine and terrestrial resources have been overlooked.

Caroline Atoll (Chapter Frontispiece) is situated at 10°00'S latitude and 150°13'W longitude in the south-central Pacific Ocean. Caroline is the southeasternmost of the Southern Line Islands, a group of three islands that also includes Vostok and Flint, lying 230 km to its west and southwest, respectively. Although anthropologically and geographically within Polynesia, Caroline is owned by the Republic of Kiribati (formerly Gilbert and Ellice Islands).

Caroline, 9.7 km long, 2.3 km wide at its widest point, and 26.9 km in circumference, is a crescentic coral ring with 39 islets centered on a continuous reef enclosing a relatively shallow lagoon. Its total land area above high water is 399 ha, with islets ranging in size from 0.02 to 107.5 ha. Islets extend along 55% of the reef perimeter. The closed lagoon, rich in marine life, contains a maze of patch reefs and remarkably clear water.

The island was “discovered” by de Quiros in 1606. Although remnants of an ancient Tuamotuan culture still exist, the atoll apparently never supported a long-term permanent population and has been less affected by man than most Pacific islands. Its European history includes guano export, a multinational expedition to observe a solar eclipse, and copra production. It has been uninhabited since the early 1930's (a factor contributing to its relatively undisturbed ecology), except for the presence of one family from 1987 to 1991. The primary factors responsible for its lack of permanent settlement are remoteness, apparent absence of usable ground water, the repeated failure of its coconut plantations, absence of a passage into the lagoon, a paucity of safe boat anchorages, and an abundance of rats.

Until the 1988 US–USSR Expedition on the *Akademik Korolev*, only one fairly accurate map was available, which named seven islets. We have drafted an accurate map based on this field work and recent aerial photographs, also naming 32 previously unnamed islets, 4 islet groups, and an inlet. During 8 days of intensive field work, we surveyed all 39 islets, walking 33 km in systematic cross-islet transects and around islet perimeters.

Soils, of coral and molluscan origin, are categorized into five types, from barren coral rubble to rubble mixed with humus and guano. Caroline provides an excellent example of soil development through different age and size classes of motus.

Caroline's near-pristine, lush native vegetation supports 27 species of plants organized into 7 plant communities—6 natural and 1 anthropogenic. The atollwide distribution of each plant species is mapped. Its insular flora, typical of central equatorial islands in their natural state, is 85% indigenous (possibly up to 93%), an extremely high figure for anywhere in the world. Though Caroline's islets are covered with extensive tracts of native woodland, the *Pisonia grandis* forests, up to 25 m high, are particularly notable as they constitute some of the best groves left in the Pacific. *Tournefortia argentea* is abundant, and *Cordia subcordata*, becoming quite rare elsewhere, is present on most islets. *Cocos* is present, but only dominates one islet; 22 islets harbor wholly indigenous vegetation.

Islets of many different age and size classes provide excellent examples of soil and vegetation development, accompanied by an increasing diversity of bird life. On account of its relatively low human disturbance and rapid recovery to a more natural state, especially over the last 70 years, Caroline is one of the few Pacific islands that is truly an "outdoor ecological laboratory." Many of its disturbed islets have recovered so remarkably they are almost indistinguishable from those that have remained pristine.

An analysis of ecological succession on motus of increasing size reveals that by the time a motu reaches 0.8 ha in size, all the natural plant communities, most plant species, and most species of seabirds are present. This is in striking contrast to species–area relationships on inhabited atolls with more introduced plant species.

For each motu, the main physiographic features, vegetation patterns, seabird colonies, miscellaneous biota (coconut crabs and rats), and the effects of human activity (if any), are described in detail. Included are vegetation maps for each motu, and tables and figures relating to species–area relationships.

Permanent protection of Caroline is currently being sought by The Nature Conservancy of Hawaii as it negotiates with the government of Kiribati for a Southern Line Islands Wildlife Preserve, which includes Caroline, Vostok, and Flint.

Geography

Caroline Atoll* (Chapter Frontispiece; Figs. 1,2) is a small, low coral atoll situated at 10°00'S latitude, 150°13'W longitude in the south-central Pacific Ocean. It lies 2,800 km south of Hawaii, 830 km north of Tahiti, and 1,030 km west of the Marquesas Islands. Its nearest neighbors are Vostok and Flint, 230 km to the west and southwest, respectively.

A recent geographic survey of Caroline by the ICBP 1990 Line and Phoenix Islands Expedition, using a compact satellite navigation computer, indicates that the atoll lies one nautical mile east of its previously charted longitude position, 150°14'W. Its range of coordinates are 09°54' to 10°01'S latitude and 150°12' to 150°14' W longitude. The actual coordinates given, 10°00'S and 150°13'W, intersect in the lower lagoon just west of the "blind passage."

Caroline is the southeasternmost of the Line Group (Fig. 1), a widely scattered group of five atolls, five islands, and two submerged reefs lying in the south-central Pacific Ocean between 06°N and 12°S latitude and 162° and 150°W longitude. Scattered across 250,000 km² of ocean, the Line Group falls naturally into two parts: the Northern Line Islands, four atolls and one reef north of the equator, and the Southern Line Islands, five islands, one atoll, and one reef to its south. The name, Line Group, reflects its equator-straddling location.

*Note: Caroline Atoll is neither physically, geographically, nor politically associated with the Caroline Islands, now part of the Federated States of Micronesia, more than 6,000 km to the northwest. Because of this confusion, we use the name "Caroline Atoll" instead of "Caroline Island."

Although archaeologically and geographically within Polynesia, the Line Group was uninhabited when discovered by Europeans; its islands have been variously claimed by the United States and England. With the exception of US-owned Jarvis, Palmyra, and Kingman Reef, all are now governed by the Republic of Kiribati (formerly Gilbert Islands).

Caroline, 9.7 km long by 2.3 km wide at its widest point, is a crescentic coral ring 26.9 km in circumference. It is composed of 39 islets (Fig. 2) and a few incipient islets, centered on a continuous reef flat, submerged at high tide, that encloses a relatively shallow lagoon. The total land area above high water is 399 ha. Entirely of coralline origin, its geology, soils, climate, and vegetation are typical of low-latitude atolls. It is relatively unmodified by man.

History of Caroline Atoll

Pre-European History: Tuamotuan Period

Centuries before Europeans encountered Caroline, this lonely atoll was inhabited by Polynesians. No oral traditions of this occupation are known, but evidence of former habitation was evident when de Quiros found the atoll in 1606. He noted "an old canoe, lying on her side," and a small grove of coconuts planted on South Island (Bennett, 1840; Markham, 1904).

No further clues to the atoll's early history were unearthed until Messrs. Brown, Brothers, and Arundel exposed about 50 ancient Polynesian sites in the 1870's while digging for guano (Holden, 1884; Arundel, 1890). Although the largest two were marked as "graves" on Arundel's 1883 map (Fig. 4), no bones, ashes, or human remains were found. Natives living on Caroline called them "marai" (*marae*). Arundel photographed and drew plans of them (Fig. 3): depicted are a platform of coral and conglomerate rock, surrounded by 10 smaller slabs resembling gravestones, all arranged in a rectangular plan. Their findings were later identified as Tuamotuan *marae* (Emory, 1947). *Marae*, according to ancient belief, "bound the ancestral spirits and gods of the kindred to the land, putting it under their eternal guardianship" (Emory, 1947). The largest *marae* was on northwest Wake Island, and a smaller one was found near the southern tip of Long Island. Both locations conform to such prerequisites for building *marae* as nearby shorelines and birds (see Description and Ecology of the Motus section [Wake Island]), which Tuamotuans believed housed divine spirits (Emory, 1947, p. 123). Although members of the ICBP 1990 Line and Phoenix Islands Expedition located them and took photographs and measurements of the Wake site (Pl. 36), no field work by archaeologists has been conducted.

Post-European History: 17th to 19th Centuries

On 21 February 1606, the Portuguese explorer Pedro Fernandez de Quiros, employed by Spain, "discovered" Caroline Atoll (Markham, 1904; Stevens & Barwick, 1930), naming it San Bernardo. Despite its remote location, Caroline was encountered early in Pacific history, long before Tahiti, Rarotonga, and Hawaii. This is possibly due to its location, for early navigators tended to sail due west from South America along lines of latitude, and 10°S was an obvious choice. De Quiros, the last adventurer in the Spanish age of discovery, was

leading his second major trans-Pacific expedition with 3 ships and 150 men obsessed with finding the fabled “Terra Australis Incognita.” The descriptions of Caroline by his crew, although at variance with one another, still apply today (Pl. 1). Their first at-sea impression was that it was “divided into four or five hummocks, and all the rest submerged. Its circumference appeared to be ten leagues” (Markham, 1904). After landing, they found that

There was a great number of fish inshore, and, owing to the water being very shallow, they were killed with swords and poles. There were great numbers of lobster and crawfish, and other kinds of marine animals. They found a great quantity of cocoa-nuts in a heap at the foot of the palm trees, many large, and of different sizes. There were a great quantity of sea birds of several kinds, and so importunate that they seemed to want to attack the men. We took plenty of all these things...It seemed to the Captain that on an island where there are so many trees there could not fail to be water. (Markham, 1904)

Fresh water was crucial to de Quiros and his crew, who were suffering from lack of food and water. Despite their efforts, however, they failed to obtain water. Disappointed and lacking energy, they continued their voyage the following morning. Their demoralized state may explain one statement that Caroline “consisted of twenty-two islets, uninhabited and without water, trees or scrub for wood.”

In 1795, Captain W. R. Broughton, on the British sloop *Providence*, rediscovered the atoll while voyaging from Tahiti to Hawaii. He named it in honor of the daughter of the First Lord of the British Admiralty (Broughton, 1804):

The southern extremity was the highest part, covered with trees, most probably cocoa-nut from their appearance, as they stood in detached clumps along the shore. The island...appeared to be low, and covered with trees, and if I am right in its estimated distance, its length will be about five miles in a north and south direction. I named it Carolina Island in compliment to the daughter of Sir P. Stephens of the Admiralty.

Because early navigation techniques and communication were far less sophisticated than today, especially with regards to longitude, Caroline was sighted or “discovered” by several more explorers who were unsure of its identity. By 1821 the atoll had amassed an impressive collection of coordinates and names: San Bernardo, Island of Fish, Thornton, Hurst’s, Clark’s, Independence, and Carolina (which later became Caroline). Some navigators equated Caroline with an island named “San Bernardo” by the Spanish explorer Mendaña in 1595. Mendaña’s island has only recently been verified as Puka-Puka in the northern Cook Islands (Maude, 1968).

The best early descriptive account of the atoll’s flora and fauna comes from an 1835 visit by F. D. Bennett, who was reasonably well versed in natural history (Bennett, 1840). He noted that the islets then, as now, were “covered with verdure...surprisingly luxuriant, when compared to the arid soil it covers.” Although Bennett had visited many atolls, he was particularly impressed with the quality of Caroline’s coral reefs. His party observed “rats of a red-brown color” and

various birds but no reptiles (Subchapter 1.2). Although he discusses “land lobsters (*Coenobita* species),” no mention is made of coconut crabs (*Birgus latro*).

First Occupation: The existence of two small coconut groves on Caroline prompted two British entrepreneurs, representing the Tahitian firm Collie & Lucett, to establish a stock raising venture there in 1846. This first known settlement was located adjacent to the main coconut grove on the northwest peninsula of South Island; a smaller grove evidently existed “on the south-south-west side” of the same island (Lucett, 1851). Tahitian laborers tended pigs, hens, turkeys, and grew many food plants, including pumpkins and melons. They dried and salted fish, planted coconuts, and extracted coconut oil (Maude, 1942a; Garnett, 1983) and were evidently still there in May 1852 (Ellsworth, 1990).

Political Annexation: Though inhabited in prehistory by Tuamotuans, officially “discovered” by the Spanish, and visited by British, French, and American ships, it took centuries for Caroline to acquire a political identity. It was formally annexed to Britain by Captain Nares, R. N., who arrived in the H.M.S. *Reindeer* in 1868, finding 27 residents.

Caroline was under the control of various merchants in the late 19th century: Lionel Brown, Captain Brothers, and later John Arundel, a well-known businessman, trader, and guano merchant in the Pacific. Arundel’s 1883 map (Fig. 4) of Caroline is the only reasonably correct chart published until this paper.

The Guano Era: Though bonded under the American Guano Act in 1860, no phosphate was dug on Caroline until Arundel was granted a 7-year license in 1874. A few months earlier, a set of moorings was laid off the lee side of South Island, allowing ships of up to 1,000 tons to lie safely during trade wind weather. Guano was the only successful business venture at Caroline: approximately 10,000 tons were shipped to California and Australia between 1873 and 1895, when supplies became exhausted (Young, ca. 1922).

Solar Eclipse Expedition: In 1883, Caroline received international publicity when astronomers calculated that it lay directly under the path of a pending solar eclipse. As a result, three parties of astronomers (American, British, and French) set up camp on South Island, making detailed observations of this celestial event (Pl. 2a). At that time Caroline was more famous, and housed more people, than before or since: 7 “natives,” scientists, and crewmen totaled 51 occupants. Legacies from former inhabitants included three houses (Pl. 2b), two sheds, three huts on smaller motus, nautical flotsam and jetsam, and two shallow wells. To this they added tents, observatory frames, a marble slab, flagpole, and brick “piers” for their telescopes, most of which remained as technological litter.

This expedition (Dixon, 1884; Holden, 1884; Holden & Qualtrough, 1884; Trelease, 1884; Young, 1884) also marked the first attempt to describe the topography, climate, flora, and fauna of the atoll. Drawings included an artist’s rendering of Caroline and map of the “settlement” (Pl. 3) and views along South Island’s lagoon shore (Pls. 4, 5). Another map (Fig. 5) was drafted but is highly inaccurate.

Observations by the astronomers on vegetation, birds, insects, reptiles, marine organisms, et cetera were sketchy (Butler & Strecker, 1884; Dixon, 1884). Dixon, the zoologist, listed such organisms as “shrimp,” “hermit crabs,” “gnat,” et cetera. As with Bennett, there was no mention of coconut crabs, even though they were evidently abundant on South Island in 1910 (Young, ca. 1922).

The Late 19th and 20th Centuries

In 1875, C. D. Voy, a naturalist from California visited Caroline, collecting mollusks (Pilsbry & Vanatta, 1905a,b) and fish (Fowler, 1901).

As early as 1885, Arundel began to clear land and plant coconuts, but his planned copra industry was unsuccessful. In 1897 he sold his business to the Pacific Islands Company, Ltd., which also failed. The coconut plantations suffered from disease and poor vitality, and populations of Polynesian rats apparently exploded. By 1904, when the H.M.S. *Icarus* visited Caroline, only six Polynesians lived there. A few months later they were repatriated to Niue, and Caroline remained uninhabited until 1916, when a new effort was made to develop the coconut plantation by Messrs. S. R. Maxwell & Co., Ltd.

During the uninhabited years, South Island’s vegetation and wildlife began to recover from the earlier forest felling (Pls. 2–4). When Mr. J. L. Young, then managing director for S. R. Maxwell & Co., Ltd. (Young, ca. 1922), visited the atoll in July 1910, he described it as a wilderness, teeming with sooty terns, fish and coconut crabs:

The ground was covered with nests of seabirds which latter rose like a cloud when disturbed: the noise of their shrieking was so great that one had to shout to enable oneself to be heard by his companions. Hundreds of great Coconut Crabs were seen: 40 large ones were caught by the crew of the schooner in an hour. The reef and the lagoon swarmed with fish and small sharks.

From 1916 to 1929, Caroline was altered more than before or since. All the available land on South was deforested to make room for thousands of palms, and laborers demolished huge numbers of coconut crabs and seabirds, which were thought to damage the palms (Young, ca. 1922). In addition, coconuts were planted on all of the main windward islets, southern Nake, and on Mannikiba. Plantation workers in great part lived off the land, feasting on fresh fish, seabirds, seabird eggs, turtles, and coconut crabs.

Copra exports averaged around 14 tons per year from 1929 to 1934, after which the company ran into debt. Concurrently, the French government forbade further recruitment from Tahiti; by 1936 only a few families were left (N.I.D., 1943). In 1941 the atoll carried a price tag of 600 English pounds (Maude, personal communication), but was never purchased.

Occupation leases for Caroline were canceled in 1943, after which the British Western Pacific High Commission repossessed it (Maude, 1953). However, new “queen’s leases” were granted to M. P. A. Bainbridge of Papeete, Tahiti (1951–1964) (Nicholson & Douglas, 1969), then Captain Omer Darr (1964–1989) of Moorea, French Polynesia. When the

British granted independence to the Gilbert and Ellice Islands in 1979, a new country, the Republic of Kiribati (pronounced “Keer-ee-bahss”) assumed ownership of Caroline, along with most of the Line and Phoenix Islands.

Apart from occasional parties of Tahitians cutting copra and a shipwrecked sailor in the early 1880’s, the atoll remained uninhabited for over 50 years. During this time, Caroline’s vegetation and wildlife recovered to such an extent that, were it not for unpublished manuscripts from Maude (Maude, ca. 1938, ca. 1942a, and no date), including Young’s (ca. 1922) “Memoranda re Tahitian Business” our detailed vegetation analysis (including tree diameters), and the 1990 comparisons with Flint and Vostok, we would have been unaware of the actual extent of previous human interference or of the rapidity of forest recovery (the fact that 60% of Caroline’s motus harbored wholly indigenous vegetation seemed to point to a relatively pristine atoll).

In 1987, the Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM, a French scientific research agency) was requested by the Kiribati government to conduct a short study at Caroline on the feasibility of pearl-shell culture (G. Monet, personal communication). Their results concluded that the atoll would be inappropriate for this type of development.

Also in 1987, a Scotsman, Ron Falconer, his French wife Anne, and two small children settled on Caroline as volunteer custodians. From October 1989 to November 1990 a new lease was under negotiation by Felix Urima, a French businessman, who planned to blast a channel through the reef, construct an airstrip, build a small hotel, cut timber, and engage in various commercial ventures including fishing, a turtle farm, and pearl-shell culture. In April 1990, Urima’s workers began commercial fishing, killing turtles and coconut crabs, and clearing land (Kepler, 1990a). This was a major new insult to the atoll which, in spite of its long history of intermittent human occupation, remains to this day “possibly one of the least spoiled of true atolls in the Pacific” (Stoddart, 1976). Reports from our expeditions to Caroline (Kepler & Kepler, 1989; Kepler, 1990a,d) resulted in the short-lived cancellation of Urima’s tentative lease in November 1990. As of this writing, Urima has returned to unlimited fishing at Caroline’s reefs. The government of Kiribati appears amenable to negotiations for a wildlife preserve (see Subchapter 1.2 [Conservation section], this volume). Conservation efforts are presently underway for Caroline to become part of a triple-island wildlife preserve with Vostok and Flint (see Subchapter 1.2 [Conservation section], this volume).

20th Century Scientific Studies: In June 1965, a field party from the Smithsonian Institution’s Pacific Ocean Biological Survey Program (POBSP) visited Caroline for 2 days (Clapp & Sibley, 1971a). Their survey and specimens added much to the previous botanical and ornithological knowledge of the island. Other quick visits were made by the Line Islands Expedition on 9–10 September 1974 and by Roger Perry, then Wildlife Warden of the Line and Phoenix Islands, on 12–13 November 1977. Eleven years later the present authors surveyed the terrestrial environments of Caroline more thoroughly than had

been previously attempted. This visit was part of the Third Joint US–USSR Bering & Chukchi Seas Expedition, a 4-month voyage that also included oceanographic studies in the Pacific Ocean and South China Sea.

In 1990, one of the authors (AKK) visited Caroline twice with the International Council for Bird Preservation (ICBP) 1990 Line and Phoenix Islands Expedition. These visits were primarily to discuss conservation matters with the Falconers; introduce Caroline to Dr. and Mrs. M. Garnett, representatives from ICBP; confirm the illegal taking of fish, turtles, and coconut crabs by Mr. Urima's men; find the Tuamotuan *maraes*; survey North Arundel Islet; collect invertebrates; and fill in missing details from the 1988 expedition.

Methods

From 22 to 29 September 1988, Drs. A. K. Kepler, C. B. Kepler, D. H. Ellis (USA), and Mr. Katino Teeb'aki (Republic of Kiribati) surveyed all 39 motus at Caroline Atoll (Fig. 2), gathering detailed information on plants, seabirds, land birds, mammals, reptiles, coconut crabs, and human disturbance. Some incidental data have been added from the two visits in 1990 (10–13 March, 18–28 May) by Dr. A. K. Kepler, Captain G. Wragg, A. Garnett, M. Linsley, J. Phillips (March), and Dr. M. Garnett (May).

Prior to the first expedition, a series of transects and known botanical information were mapped to ensure that 5% of each motu was sampled and to maximize our chances of encountering all known plant species. Transects on the larger motus (Nake, Long, South) were spaced approximately 400 m apart and, with one exception, were perpendicular to the long axes of each islet (Tr. 3 on Nake extended first from east to west, then ran south parallel to the west coast). If the motus were greater than 400 m long, we used two transects. Transects on the smaller motus passed through their widest points (Fig. 8). Their lengths ranged from 77 m (Azure) to 2,000 m (Tr. 3, Nake).

Considerable modifications were required when we realized that the Clapp & Sibley (1971a) map (Fig. 7) was incorrect. We redrew the transects on Arundel's 1883 map (Fig. 4), secured just prior to the expedition. On South Island, due to impenetrable draperies of *Ipomoea* vines, Tr. 3 was omitted, Tr. 5 ran only from the lagoon south to the *Ipomoea* curtain (75 m), and Trs. 4 and 6 ran north and south until we reached an impasse (Pl. 7).

Compass headings were determined by the configuration of each island. Beginning at high water mark, all distances (islet dimensions, widths of reef flats and substrates, and plant communities) were measured using hip chains with biodegradable cotton thread. These parameters were later checked against aerial photographs in stereoscopic pairs taken in 1985 by the Royal New Zealand Air Force (RNZAF), which provided 3-dimensional overviews of every islet. Vegetation maps for each islet were constructed by drawing the outlines and plant communities (based on the aerial photos) on graph paper, enlarging, then counting dots.

Data were collected in a 30-m (15 m to each side of the transect) swath along each transect and recorded on field forms. Within each plant community we took photographs,

assessed the relative abundance of each plant species (rare, uncommon, common, very common, abundant, and locally common; see Vegetation section) and recorded plant community width, plants collected, and substrate type. We also estimated the maximum height of the dominant vegetation and percentage of ground area covered by each species.

In addition to the linear transects, an additional 19,300 m of perimeter surveys were conducted on 21 islets (Fig. 9). The combined distance for linear and perimeter transects was 32.6 km. Seven tiny islets (Noddy Rock, Skull, Atibu, Bo'sun Bird, Coral, Reef-flat, Fishball) were surveyed completely.

In 1988, we camped on the atoll for seven nights, establishing base camps (Fig. 8; Pls. 6,8) on the northwest point of South (22–24 September) and southwest Long (25–28 September). We relocated camps using a Zodiac with outboard motor and an inflatable Sevylor canoe (Pl. 9). All transects were surveyed during daylight hours, beginning at dawn. Walking the interislet channels was relatively easy at low tide, but became hazardous at incoming or high tide, as the numerous black-tipped reef sharks, *Carcharhinus melanopterus* (Pl. 10), regularly charged at our legs and had to be beaten off with sticks and coral chunks.

During the 1990 visits, we stayed on Motu Ana-Ana with the Falconers. Work was not intensive, as in 1988. We walked or motored an inflatable Lancer, visiting 20 motus: Ana-Ana, Kimoa, Pisonia, Eitei, South, North Arundel, Noddy Rock, Brothers, North Brothers, Skull, Pig, North Pig, Bo'sun Bird, Long, Nake, Mouakena, Shark, Scarlet Crab, Bird, and Fishball. Insects were preserved in ethyl alcohol. We used a "Magellan" NAV 1000 to obtain accurate geographical coordinates of Caroline.

Naming Caroline's Motus

Previous literature has provided vague or incomplete data on Caroline's constituent motus (Bennett, 1840; Holden & Qualtrough, 1884; Markham, 1904; Stevens & Barwick, 1930; Bryan, 1942; Clapp & Sibley, 1971a; Garnett, 1983). This confusion resulted because most previous visits had been brief. The only charts available were a quite accurate survey by Arundel, a guano merchant who mapped the atoll in 1883 (Fig. 4; Admiralty Chart, No. 979, 1965), and a map, greatly in error, drafted by an international Solar Eclipse Party, also in 1883 (Fig. 5). There are no hydrological navigation charts. Unfortunately, the eclipse party map has been used in all subsequent scientific, historical, and sociological publications (Bryan, 1942 [Fig. 6]; Maude, 1968; Clapp & Sibley, 1971a [Fig. 7]; Garnett, 1983). It shows only 25 of the 39 islets and many of the shapes are distorted. The 38 islets on Arundel's map are similar to those in the RNZAF (1986) aerial photographs. Only a few islets appear to have changed in minor ways since 1883: major discrepancies in Arundel's map, we believe, are due to difficulties involved in the accurate rendition of small land areas (i.e., the South Nake Islets). Maude (ca. 1938) counted 36 islets but never published his information.

To aid our survey we named 32 islets and 4 islet groups (Fig. 2). Our names, whether in English or Gilbertese, reflect appropriate aspects of islet biology. Etymology is provided in

the Description and Ecology of the Motus section. Gilbertese names are prefixed with *motu*. Any name not appearing on Arundel's map (Fig. 4) was given to the islets by us. They have been sent to the British Admiralty and US Hydrographic Office (along with corrections to the Pacific Pilot) for official recognition.

Structure and Topography

General Account

Caroline, one of the oceanic islands contributing to Darwin's theory of atoll formation (Darwin, 1842), is a low island derived entirely from coral reefs and mollusks, living and dead. Although undoubtedly resting upon an ancient basaltic base, today's atoll reveals no visible fragments of its volcanic heritage. "The atoll consists of a chain of twenty-five [*sic*] little islets, well covered with trees and shrubbery, the whole forming a quiet scene of grove and lake, charmingly set off by the contrasting ocean" (Holden & Qualtrough, 1884). This description could apply equally well today. Caroline is actually composed of a ring of 39 "permanent" and 3 incipient islets whose total area is 398.94 ha. Most are well wooded, but four tiny ones, less than 0.1 ha in size, are scarcely more than coral rubble piled on the reef, supporting sparse patches of *Tournefortia* and *Heliotropium*. One islet, Noddy Rock (Pl. 19), is a vestige of a former reef segment.

Our terminology is based on Tracey *et al.* (1955) as cited by Wiens (1962), to which we have one addition. The name *motu*, Polynesian for "islet" or "small island," is now a technical term for detrital reef islands (Danielsson, 1954; Stoddart & Gibbs, 1975). In this paper the terms *motu* and islet are used interchangeably; however, as *motu* is now a *bona fide* English word and not italicized, it may be pluralized by adding an "s" (normally Polynesian words are not pluralized with "s").

Caroline's overall shape is like a flattened crescent, 9.7 km long on its north-south axis. Its perimeter is 26.9 km, measured along the outer reef. Its greatest breadth (including both reefs), 2.3 km, lies centrally along an east-west transect that includes Motu Mannikiba and lower Long Island. The longest islet, Long, extends 4.23 km from north to south, while South Island, extending 1.2 km from east to west, claims the widest stretch of land.

The motus, lying upon a wide, continuous reef flat which encloses an elongated, relatively shallow lagoon, fall naturally into groupings of 3 large islands (South, Nake, Long) and 4 groups of smaller islets (13 Windwards, 5 Southern Leewards, 11 Central Leewards, 7 South Nakes). There are four basic motu shapes:

1. long, linear, and parallel to the reef axis (e.g., Long Island);
2. small, linear or oval, and perpendicular to the reef axis (e.g., Southern Leeward Islets);
3. triangular or crescentic, with the apex facing the seaward reef (e.g., most of the Windward Islets); and
4. large and quadrangular, occupying the ends of the atoll (e.g., South, Nake).

All individual motus are discussed in detail in the Description and Ecology of the Motus section.

Reef Flats

Caroline's peripheral reefs, which completely surround the lagoon and upon which the motus rest, are consistently wide (average 562 m, range 396–759 m, $N = 100$). The windward and leeward reefs differ in structure and dimensions. Neither are entirely dry, even at the lowest tides. They consist primarily of barren calcareous rock, which on other atolls generally represents the erosional surface of an older reef. Jagged "mushrooms" of newer (but dead) reef dot the leeward reefs (Pl. 11). There are no passes from ocean to lagoon, a typical feature of central Pacific atolls (Wiens, 1962). The combined area of intertidal and subtidal marine environments that they enclose is several times the area occupied by terrestrial habitats.

In the Southern Hemisphere, reef flats tend to be widest in the southwest sector and narrowest in the northeast (Wiens, 1962). Caroline's reefs are quite wide throughout the west (Pl. 12), and definitely narrowest in the northeast off Nake (Pl. 13).

The reef rim, irregularly dentate and 26.9 km in circumference, is surmounted by islets for 55% of its length. On 72% of all Pacific atolls, less than half the reef circumference is occupied by land (Wiens, 1962). Caroline lies within a 28% minority in which one-half to two-thirds of the reef rim contains land. Corresponding values for 2 Tuamotuan atolls, Rangiroa and Raroia, are 33% and 35% (Stoddart & Sachet, 1969). Where motus exist, the reef flat is divided into the seaward reef flat (Pl. 12), islet, and lagoon reef flat (Pl. 14).

At low tide all reef flats are wadable. Black-tipped reef sharks were a threat to our safety in most areas in 1988, but by 1990 dozens had been killed. The reef segments that separated the Southern and Central Leeward groups and the Leeward and South Nake groups were particularly hazardous. Within these islet clusters, names such as Blackfin, Shark, and Danger reflected this ubiquitous feature of Caroline.

The only tidal measurements taken were by the Solar Eclipse Party (Holden & Qualtrough, 1884), who noted that in May 1883 the greatest daily fluctuation ranged from a maximum of 475 mm (1' 7") to a minimum of 125 mm (0' 5"), similar to that (around 2') in the Tuamotus (Stoddart & Sachet, 1969); Arundel's map (Fig. 4) gives 0.5 m (1.5') for Caroline, which we have tentatively used in the schematic profiles (Figs. 34–36) as the difference between low and high spring tidal levels.

Windward Reef Flats: Constantly pounded by surf (Pl. 16), the windward reefs are typically narrower than those to leeward, averaging 519 m (range 396–759 m), though this is less evident from a map than in the field.

The windward reefs are 13.5 km long, surmounted by 16 motus that total 63% of its length. This is not surprising, as a recurrent pattern on central Pacific and Tuamotuan atolls is that motus are more frequent along windward reef rims (Thomas, 1961; Wiens, 1962). The longest islets are Nake (1,980 m) and Long (4,226 m), both formed from the coalescence of two or more smaller islets (Figs. 37–39). The rest vary from 18 m to 858 m in length.

The character of these reef flats differs, depending on the presence or absence of land, interisland distances, lagoon depth, and recent weather conditions. In February 1990, part

of a hurricane hit Caroline, rearranging tons of coral rubble and sand on the windward beaches and motus, tearing out *Tournefortia* scrub, obliterating much of the native herb mat, exposing beachrock, depositing large chunks of broken reef on the seaward reef flats, and changing the sizes and shapes of the beach crests.

Reef Rim with Motu: The width of the seaward flats is quite uniform, averaging 307 m (range 193–396 m), occupying 57% of the rim width. It consists of a slightly raised algal ridge bearing the brunt of incessant wave action and a rubbly reef flat, partly drying at low water, which sweeps up to the motu's beach (Pl. 16). Adjacent to Nake, in the northeast, the seaward margin forms a shallow moat separating the land and algal ridge (Pl. 13).

The motus differ considerably in width, ranging from the narrow tip of Long, merely 30 m wide, to Windward, 290 m wide. Nake and South islands, forming "caps" to the atoll at its upper and lower ends, respectively, exhibit characteristics more typical of windward than leeward motus. Because coral debris accumulates wherever atoll reefs turn sharply (Thomas, 1961), these two motus are the widest on the atoll (Pls. 16, 17). A comparison of maps a century apart (Figs. 2, 4) indicates that several layered ridges of coral debris have accumulated on northern Nake since 1883.

Reef Rim without Motu: Zonation within the reef flat is less marked where there is no land. Within these interislet reef flats, however, certain areas of high water transport have carved surge channels and grooves. These are particularly evident at the north and south ends of islets (Pl. 18), between islets, and within the longer flats. In all these areas, tidal fans extend into the lagoon especially at its northern end where sedimentation is most active. Caroline has no deep pass or navigable channels into the lagoon nor a ship anchorage beyond the reef, though small boats may anchor within the close lee of South Island during normal trade winds and low seas. Landing in an inflatable is best made across the reef slightly north of the "boat entrance" (marked by an upright anchor).

The reef flat between Tridacna and South Island, serrated with 6 erosional grooves, one labelled "blind passage," is of particular importance to navigators. Its most southerly channel is a narrow diverticulum 380 m long within a reef 430 m wide. On all previously published maps this passage is drawn as though it completely connects ocean and lagoon (Figs. 4–7). However, it is a true blind channel (Fig. 50), serving as a sheltered anchorage for motored yachts near its lagoon end, but cannot be entered or exited during high winds or moderate-to-high surf.

Leeward Reef Flats: These are wider, flatter, gentler, more consolidated, and less filled with rubble than the windward reefs (Pl. 11). Everywhere except within the surge channels, an orange-colored alga blankets the coralheads, chunks of upraised coral (Pl. 11), carbonate rock, and giant clams. This alga is found on many atolls—for example Enewetak and Rangihoa (Stoddart & Sachet, 1969; US Department of Energy, 1987). Living coral is sparse.

Surge Channels: These occur in a variety of shapes and sizes, depending on the distances between motus, the extent and buildup of reef flats adjacent to land, and lagoon depth. Surge channels and reef grooves (*hoa*) are deeper on the windward side. Aerial photos indicate that the vigorous currents washing daily into Caroline's lagoon have created larger debris fans between windward motus than between those to leeward (see Chapter Frontispiece).

Beaches

Caroline's beaches—the zones lying between low water mark and the inland limit of wave-deposited debris—are entirely of reef origin. There is, however, considerable variation in the sizes of coral rubble, and the proportions of sand and silt with which they are mingled. In general, the windward beaches and surge channels, subject to winds and swells and in a constant state of erosion or deposition, support the greatest variety of sediments: well-sorted sands; gravels of coralline, algal, and molluscan origin; and a wide variety of sizes of coral rubble.

Almost all exposed rubble on Caroline is colored from pale to dark gray, a consequence of penetration by cyanobacteria (Fosberg, 1953). Typically the oldest rubbles, highest up the beach and extending into the interior, are darkest. A marked beach crest rises—gently or abruptly—from the windward beaches, at the crest of which is deposited an assortment of flotsam and jetsam: bottles, plastic, wood, coconuts, et cetera (Pls. 16, 20). No large chunks of disengaged reef were found on or near land in 1988, but in 1990 many of these littered the windward reefs and shores, the result of cyclonic weather in February of that year. Similarly, in 1990, considerably thicker deposits of coarse sand had overlain the rubbly windward beaches and interislet channels of 1988.

Alterations to Caroline's beaches provide the major areas of change in islet shape. The main areas of aggradation are on the northwest and southwest leeward points of the windward islets. This is particularly true of the larger ones such as Brothers (which has joined with a separate islet mapped by Arundel), and Windward and Tridacna (which have added more sediment to their southwest points during the last century).

Beachrock: These narrow, elongated strata of eroded upraised reef, brown consolidated sands, and reef detritus are not abundant on Caroline. Occurring as strips at the low water mark, they flank the windward beaches of Nake, Long, and South (Figs. 37, 38, 50; Pl. 58) and a few of the leeward islets. They become more exposed after violent storms. Extensive areas of a coarser conglomerate (Pl. 21) hug the inner reef flats of western South Island.

Upraised Reef: In a few areas, jagged, eroded upraised reef (*champignon* or *feo*) is evident—for example, the lower quarter of Long. A thin soil cover supports a forest of lower stature than would otherwise be expected. In this minikarst area the rocky substrate is pitted with holes of varying sizes and undermined with subterranean tunnels in which at least two species of land crabs (*Birgus latro*, *Cardisoma* spp.) shelter (Pl. 22). Noddy Rock (Pl. 19), the smallest motu (0.02 ha), and

many jagged coralline “mushrooms” found on the reef flats (Pl. 11), are probably remnants of former reef flats formed when sea levels were several feet higher than present.

Lagoon

A notable attribute of Caroline’s lagoon from a conservation perspective is its outstanding clarity and beauty. Throughout, but especially near the Central Leeward Islets, the twisted reef configurations studded with white sandy channels and deeper circular openings generate a spectrum of stunning colors—turquoise, apple green, tawny, azure, and royal blue (Pl. 25).

Caroline’s lagoon, 8.9 km long, is closed. Though it appears to dominate the atoll, its total area is less than that of the combined reef flats. The lagoon is relatively shallow, tapering in shape and depth at each end, and is crisscrossed with living coral. Its bathymetry is unknown.

In the north the lagoon is more sheltered, as the presence of continuous vegetated land buffers the easterly trades. At its northern extremity, merging reef flats squeeze the lagoon until it disappears east of Pandanus Islet. A filled-in portion of the former lagoon penetrates Nake for 300 m as a fishhook-shaped mudflat, Sandy Inlet (Fig. 37, Pl. 23), before succumbing to encircling vegetation. At the lagoon’s southern end, where winds whip through the “blind channel,” it is choppy, having more sediment and slightly less visibility. However, within the lee of South Island’s north-central curve, the lagoon is frequently quiet and reflective (Pl. 24).

Lagoon Hydrology: Although Caroline’s hydrology has not been studied, it has been closely observed for over two years by Ron Falconer, especially the south end of the lagoon and “blind passage.” He has noticed that the lagoon water is typically “perched” at a level above that of all but the daily high tides. High tide water flows rapidly over the reef flats into the lagoon but is held back by the reefs as the tide lowers. Ron has noted that lagoon water at low tide is about 0.3 m higher than water in the “blind passage.” Water moves out of the lagoon through a few channels that, although deep in places, form broad, shallow troughs over the reef flats. A major channel with a current flowing west at several knots passes along the northwest point of South Island, although water passage is impeded by the reef flats west of South Island. If a channel were to be blasted through the reef flats, as has been proposed, this delicate hydrology would be disrupted. For example, the high tide water is never more than 20 cm above the coral heads and reefs in the lagoon. A man-made reef channel for vessels could lower water levels 30–40 cm, thereby exposing and killing the extensive *Acropora*–*Tridacna* reefs within the lagoon.

The “blind passage” northeast of South Island (Fig. 50) is sustained by a powerful northward flow of water along the east coast of South Island and a strong southward flow of water along the seaward reefs of Tridacna Islet. The South Island flow is apparently augmented by water draining from a large shallow basin on the reef flats south of the island. Water spills into the “blind passage” and drains east at about 4 knots against the prevailing trade winds and surf. There is much less current at the west (inner) end of the passage, where less water is collected, and throughout the passage at low tide (there being essentially no water flow out from the lagoon).

Patch Reefs: A complex series of patch reefs and coral knolls (primarily *Acropora* spp.), circular and elongated, flank the smaller motus and crisscross most of the lagoon’s area (see Chapter Frontispiece). They are particularly evident in the southern two-thirds of the lagoon, where they approach and/or break the surface. Coral limestone bedrock, surmounted by a variety of living coral, mollusks, and other invertebrates, provides their basic structure (Fig. 10). The atoll’s perimeter reefs shelter the knolls from storms, surf, and excessive erosion.

Caroline’s lagoon is gradually filling in with ever-expanding patch reefs and debris washed in from the fringing reefs. Since Arundel’s time, the effects of detrital deposition can be discerned as changes in the shapes of islets such as Nake, Danger, and Arundel (compare Figs. 2 and 4).

Such change is typical of atoll evolution. Geologically, Caroline is a few steps behind one of its “neighbor” Line Islands, Christmas, where sediments and coral growth have converted the original lagoon into a maze of supersaline, minilagoons and tiny islets, mostly cut off from the sea. Further steps in evolution are exemplified by completely filled-in atolls such as Jarvis and Vostok, where not even salty pools remain.

Tridacna–Acropora Reef: Though the giant clam (*Tridacna maxima*) is an abundant component of Caroline’s lagoonside reefs, exceptional aggregations flank the most southerly windward motus (Brothers through Tridacna, Figs. 44 to 48). Two especially outstanding reefs extend across the lagoon from Tridacna to Ana-Ana (Fig. 10; Pl. 26) and Tridacna to Kimoa (Fig. 48), where *Tridacna* are attached to *Acropora* spp. corals, a favored substrate (Braley, 1987). Abundant inshore *Tridacna* on all these islets suggest that their density is similar to that on the main reef: up to 20/25 m² (i.e., 80/m²), averaging 35/m² for the entire area surveyed (Sirenko & Koltun, Subchapter 1.4, this volume). This exceeds the highest densities known: up to 60/m² at Reao Atoll, Tuamotu Archipelago (Richard, 1985). Densities of 6–20/m², at Takapoto Atoll (Tuamotus) are considered high. Throughout Caroline, the clams averaged 18 × 10 cm in size. Several species of giant clams have suffered greatly in the Indo-Pacific from poaching and overharvesting; few undisturbed populations exist (Braley, 1987). Caroline is thus a special refuge for *T. maxima*.

Lagoon Reef Flats: These vary considerably but are narrower and more gently sloping than the seaward reef flats. They are typically covered with fine coral gravel and coarse sand. In sheltered areas (lower Long, Windward, Crescent, South, upper end of lagoon), lush shrubbery—*Cordia*, *Tournefortia*, *Pisonia*, *Cocos*—overhangs the lagoon. Here fine silt, sand, and/or an algal slime are common (Pl. 28). In 1988, narrow, sandy beaches occurred only on the north shore of South (Pl. 24) and east side of Shark (Pl. 29), but in 1990, sand was more common throughout Caroline.

Where the lagoon shorelines are less sheltered and vegetation does not overhang the lagoon, unvegetated rubble and sparse herb mats are typical. Here, lagoonside rubble averages less than 2 m wide (Pl. 31). This contrasts with their seaward reef flats, which average 21 m wide (Pl. 12).

Lagoon Reef Fauna: A Brief Summary: Caroline’s marine environment is rich yet essentially undocumented; knowledge of its ecosystems is limited to small, outdated lists

of fish and invertebrates (Dixon, 1884; Fowler, 1901; Pilsbry & Vanatta, 1905a,b). However, preliminary studies on mollusks, benthic invertebrates, and lagoon plankton were begun by Soviet scientists in 1988 (Tsyban & Smith, 1988; Sirenko & Koltun, Subchapter 1.4, this volume). The lagoon and reefs are remarkably pristine, having changed little since their first discovery; all early travelers remarked on their beauty, abundance, and variety (Bennett, 1840; Markham, 1904).

The usual assemblage of tropical invertebrates—echinoderms, mollusks, crustaceans, porifera, corals, tunicates, et cetera—are present. Large numbers of black sea cucumbers (Pl. 10), about 20 cm long, are particularly abundant on the lagoon reef flats of the southern windward islands. They have been tentatively identified as *Ludwigothuria* sp. (B. Sirenko, personal communication). Conspicuous fish families include parrot fish (Scaridae), butterfly fish (Chaetodontidae), surgeonfish (Acanthuridae), damselfish (Pomacentridae), pufferfish (Tetraodontidae), and wrasses (Labridae).

Substrata

Throughout the atoll, the substrata reflect a coralline origin. There is little “soil” in the accepted sense. Various grades of jagged, eroded coral and molluscan rubble (from fist-sized to tiny pebbles), together with sand, coralline algae, and small proportions of organic litter, humus, and guano, are present. Such accumulations of reef and terrestrial debris are similar to those of other low, coral atolls (Fosberg, 1953; Stone, 1953; Wiens, 1962; Niering, 1963; Stoddart & Sackett, 1969; Reese, 1987; Garnett, 1983).

Generally speaking, atoll soils are calcareous and extremely immature, a consequence of their limited age and frequent disturbance by storms. Barely modified beyond the reef that spawned their presence, they are composed primarily of calcium and magnesium carbonates. Water retention, if any, is due to accumulated organic matter and its associated chemical changes. This is particularly important with respect to guano, which reacts with coral sand and humus to form phosphatic hardpan and nitrogen-rich “soils” (Fosberg, 1953).

Reese (1987) categorizes atoll “soils” into five types, all of which occur, in different proportions, at Caroline. The degree of organic matter, decomposition, amount of humus, and the depth of the “soil” strata are directly correlated with age and size of the motus.

1. *Accumulations of coral rubble, mainly of stone size.* These youngest of “soils” are most evident around the edges of the motus, acting as a substrate for pioneer herb mats. Often extending well inland, they can support surprisingly lush *Tournefortia* scrub.

2. *Unaltered coral sand and gravel.* Although exposed sand was uncommon at Caroline in 1988, this substrate occurred intertidally where the lagoon was filling in and on actively growing sandbars, primarily in the upper lagoon (Pls. 23,28), northeast and northwest South (Pls. 24,32), and the lagoonward edge of Shark (Pl. 29). In 1990, sand was more ubiquitous on Caroline as a result of the deposition of tons of sand during the severe February storm.

3. *Soils with a weakly developed A-horizon, with color only slightly darker than the unaltered sand below, but with no*

evidence of structural development. Especially evident in 1988 within the ancient interislet channels that compose Long Island (Pl. 33), much of this substrate is now storm-eroded and overlain by fresh sand.

4. *Soils with a more developed A-horizon, deeper and darker than above, with some structural development.* This stage defines areas where the rubbly/sandy substrate approaches a true, but poor, “soil.” As such, it represents older, more stable parts of each island. It is common within the islet interiors where *Pisonia* is (or was) present. Humus and guano fill the gaps within the irregular shapes of eroded coral. Its composition may be likened to a coarse mixture of gravel, sand, bones, and shells, all mixed with sparse amounts of partly-decomposed litter. Land crabs are particularly numerous, helping break down organic matter into finer particles.

5. *Soils with an accumulation of raw humus on the surface and with a relatively deep A-horizon. During this stage phosphatic hardpan may develop.* These true soils, though somewhat depleted by guano diggers, cover significant areas on South and Nake. *Cocos* and/or *Pisonia* debris adds greatly to their dark color and moisture content. This earthy substrate is composed primarily of rotting *Cocos* fronds and fibers that have been shredded by coconut crabs. Patches of blackish muck on South Island support local patches of Polynesian arrowroot (*Tacca leontopetaloides*).

On Caroline, hardpan (Pl. 76) was present in several areas (primarily South, Nake, Long, Emerald, and Mannikiba), supporting herb mats and *Tournefortia* scrub. This substrate may be likened to an old asphalt road.

Caroline provides an excellent example of the progression of soil development through islets of different age and size classes (see Ecological Succession section). From a wave-washed mound of coral rubble, barely above sea level (Fig. 5), the substrate gradually improves in texture and fertility as the emerging islet ages and organic matter accumulates. Pioneer plants are hardy, salt-tolerant, low-lying mats consisting primarily of *Heliotropium*, and later, *Tournefortia*. Increasing numbers of shrubs provide shade and branches for nesting seabirds. Larger trees (*Pisonia*, *Cordia*, *Morinda*) add more shade and thereby increase humidity, as well as provide opportunities for additional organic “fallout”: leaves and bird remains (nests, eggs, chicks, droppings, regurgitated food, dead adults).

Each stage of substrate development accelerates the accumulation of organic material and helps to define an emerging, deeper A-horizon. Soil maturity is indicated by more organic matter, improved soil texture, and a lowered volume of coralline and molluscan debris. Caroline’s soils barely exceed several centimeters in depth and are always intermingled with coral fragments. As a result, they are unsuitable for burrowing seabirds, such as petrels and shearwaters.

Hydrology

Hydrological information is essentially lacking. No standing fresh water exists. The quality, extent, and salinity of the freshwater lenses, as well as their variability according to tide, season, and rainfall, are unknown. At the time of Caroline’s

“discovery” (1606), de Quiros and his party were desperate for fresh water. After noting how lush and green Caroline was, they expected to find good water supplies, but there was “nothing but salt water in the holes they dug” (Markham, 1904). Maude (1968) suggested, in retrospect, that had they waited longer the salt water in their shallow wells might have run fresh, as has been his experience on some other atolls. During the 19th century, three wells were used—one on Nake and two on South (Holden & Qualtrough, 1884). One South Island well contained fresh water at 1.5 m depth in 1974 (Garnett, 1983). We saw no wells but located concrete cisterns, one built near the northwest point of South in 1937 and rebuilt by the Falconers in 1989, and another uncovered one (dating from 1938) within a *Cocos-Pisonia* grove along Tr. 2, about 200 m east of the southwest corner of Nake.

Caroline’s paucity of fresh water may be partly responsible for the lack of a permanent population. The annual rainfall in 1989 (Appendix 2) was 1,242 mm (48.9”). However, like the similarly lush Nikumaroro and Orona (Phoenix Islands), Caroline’s rainfall may vary greatly from year to year, resulting in undependable water supplies. In the past, residents relied on rainfall catchment for fresh water (Maude, ca. 1938; R. Falconer, personal communication).

Shallow sources of fresh or brackish water may be present on most islets, as *Pisonia* forests occur on 74% of them, but very little is known of freshwater lenses supporting *Pisonia* forests (Wiens, 1962). If we assume that *Pisonia* is not salt-tolerant, small water lenses may be present on motus as small as 0.2 ha. This is further discussed in the Ecological Succession section.

Climate

Meteorological records for Caroline were sparse until 1989, when Ron Falconer began daily records of rainfall and wind direction (Appendix 2). Some data is available from the plantation years 1916–1920 (Young, ca. 1922) and during the 1883 Solar Eclipse Expedition (20 April–8 May) (Upton, 1884), when 203.2 mm (8”) fell. The best generalizations on weather conditions in this area are found in the *Geographical Handbook Series: Pacific Islands, Volume 2* (N.I.D., 1943), Wiens (1962), Seelye (1950), Taylor (1973), and various papers on the Tuamotus (Stoddart & Sachet, 1969; Sachet, 1983). Islands in the Line Group experience a wide range of climates. In general, those near the equator are dry, with rainfall increasing with increasing latitude north or south.

Caroline experiences a tropical oceanic climate that varies little during the year. Temperatures are uniformly warm to hot, normally tempered by trade winds from the southeast to northeast. Falconer (personal communication) has recorded an annual average of 30°C (86°F) (range 26–31°C [78–88°F]). Mean annual temperatures for the Central Equatorial Islands lie between 24° and 29°C (75–85°F). Surface temperatures increase rapidly in early morning and remain hot throughout the day. Forest interiors are humid. The daily range of temperatures exceeds the annual fluctuation in the daily mean.

Atmospheric pressure, sunshine, and cloud cover are probably similar to the northern Tuamotus—uniform except

during storms. During our 1988 surveys the sky and air were extremely clear, but we experienced much heavy cloud and rain in March 1990, the aftermath of cyclones “Peni” (entered near Vostok) and “Ofu” (entered further west).

Wind and Rainfall: Caroline is dominated by trade winds. As on all low atolls, land topography has no appreciable effect on weather. Although it lies within an area primarily influenced by southeast trades, there is a small annual oscillatory movement northward and southward, so that in reality winds blow from the east, northeast, and southeast. This accounts for the east and northeast winds that puzzled the eclipse party, who were expecting winds from the southeast (Upton, 1884). Data from Falconer (Appendix 2) indicates that, at least for 1989 and 1990, winds blow primarily from the north and northeast, and rarely from the southeast (April–August).

The atoll lies within a belt of variable rainfall, along with Vostok, Flint, and the northern Tuamotus. Young (ca. 1922, p. 13) notes that Caroline’s rainfall is “certainly less than that of Flint,” giving exact figures for 1919 (2,172 mm) and 1920 (1,854 mm) and estimates that there was “probably not more than 50” (1270 mm) during 1916, 1917, and 1919. These estimates were based on exact figures from Flint (1,600, 1,346, 1,295 mm, respectively). Falconer measured 1,242.1 mm (48.9”) in 1989 and 2,209.8 mm (87”) in 1990. An unusually stormy February in 1990 brought 640 mm (25.2”) of rain. Rainfall distribution isohyets (Taylor, 1973) assign Caroline an annual precipitation of approximately 1,500 mm (60”), a perfect average of the above 6 years (\bar{x} = 1,513 mm). In general, “winter” (May–October) corresponds roughly to a dry season and “summer” (November–April) to a wet season.

Hurricanes and Tsunamis: Atoll islets are active structures, undergoing repeated death and rebirth. Violent storms contribute to ongoing erosional and rebuilding processes. Storms deposit debris not only along the shores of the windward islets (Pls. 17,20) and across reef flats into the lagoon but sweeps it far inland.

Although the south-central Pacific is relatively free of cyclonic storms (cyclones, typhoons, hurricanes), they do occur with enough frequency and devastating force that any discussion on climate should include them. Although detailed records of hurricanes and tropical storms exist for the inhabited Tuamotus since European discovery, many of these may not have affected Caroline. However, the following evidence suggests that Caroline experienced two major hurricanes last century and that periodic violent storms can modify the atoll substantially:

1. *Between 1822 and 1825.* When de Quiros visited Caroline in 1606, the northwesterly *Cocos* plantation on South Island was healthy. When Bennett arrived in 1834, he noted that all the palms were “of dwarf stature,” and that “amidst the original groves, the number of vigorous seedlings fully confirmed Captain Stavers’ statement [who had visited the atoll in 1828] that these palms had increased greatly since his last visit to the spot” (Bennett, 1840).

A few years before 1828, therefore, something had affected the palms. By 1834 they were all of an even height and quite short, yet bore nuts. French records indicate that two devastating

storms whipped through the Tuamotus during this time—in 1822 and 1825 (Sachet, 1983). At least one of these could have affected Caroline.

2. *The 1878 cyclone.* The first unambiguous record of major devastation at Caroline comes from the letter of a certain J. M. Salmon, dated 1883 and reproduced in Holden (1884). Speaking of the time when Messrs. Brown and Brothers took possession of Caroline (somewhere between 1865 and 1872), he stated that “it seemed as if there had been a storm or hurricane at some short period previous, which had desolated the place.” Arundel (1890) attributed this to a tidal wave that swept across the Pacific from South America to New Zealand and Australia in 1868 (Arundel, 1890), but atolls do not generally suffer greatly from tsunamis because they lack focusing relief. Hydrographer of the Navy (1931, Vol. III, p. 154), however, referring to Caroline, clearly states that in “1878 a cyclone passed over the islands, destroying most of the coconut trees.”

The Great Britain Naval Intelligence Division (N.I.D., 1943, p. 490), in reference to Caroline, also states that “in 1878 a hurricane wrought great destruction.” This was possibly the storm of 6–7 February 1878, an extremely violent one which killed 117 persons on Kaukura Atoll, 750 km southeast of Caroline in the Tuamotus (Sachet, 1983).

3. *The 1990 storms.* We know from Arundel’s chart (Fig. 4) that no major islet-altering storm has hit Caroline Atoll since 1883. However, our second visit to Caroline was 2 weeks after cyclone “Peni,” centered near Vostok (February 1990), affected the atoll. Violent winds, torrential rain, and high seas had uprooted vegetation in some windward areas and greatly altered Caroline’s shorelines, interislet channels, tidal fans, and incipient islets from our 1988 visit. Sand and rubble had been rearranged on both windward and leeward islets. Motu Atibu virtually disappeared, and the main interislet channel that divides Long Island had lost its herb mats and many *Tournefortia* shrubs, becoming smothered with fresh sand.

Because islets on coral atolls rarely exceed 5 m in elevation, the tidal surges associated with Class IV or Class V hurricanes, often exceeding 5 m in depth, can overwhelm them, not only altering or destroying the vegetation, but in extreme cases completely removing them from the coral rim (Frishie, 1944). It is essential to consider the ephemeral nature of Caroline’s islets in the discussions that follow.

Sea Conditions: Because the most extensive coral rubble deposits occur around northern Nake and southern South Island, and because the *Cocos* plantation of northwest South was so badly hit by storms last century, the following Tuamotuan generalities (Newell, 1956) probably also apply to Caroline:

1. prevailing trade winds from the east give heavy seas on the northeast or windward side;
2. southern ocean swells generated in the sub-Antarctic break heavily on the south or seaward side; and
3. occasional hurricanes or tropical storms strike in the northwest or stormward quarter.

Vegetation: Vascular Plants and Floristics

Botanical History

All early visitors to Caroline described a well wooded atoll with numerous islets whose vegetation extended to the shoreline. It has changed little in the 384 years since its Western discovery. The first botanical collection and notes were those of Bennett in 1835 (Bennett, 1840), who recorded 10 flowering plants and a fern and planted Tahitian chestnut, sweet potato, and Polynesian arrowroot. The location of his plant collection, if it still exists, is unknown (Clapp & Sibley, 1971a). Evidently only a single nonnative species (*Cocos*), surviving as two small groves, persisted until the late 19th century. Beginning in 1885, coconuts were planted extensively on South Island and south Nake, but the copra industry failed twice, and from 1929 to 1987 the atoll was essentially uninhabited.

Dixon made the first true botanical collection in 1883 during the Solar Eclipse Expedition (in Trelease, 1884). All specimens were from South Island except *Laportea ruderalis*. His collection included several ornamentals and vegetables that have not been reported since, an important point as these temporary introductions have since been cited in the literature as part of Caroline’s 35 plant species. Many were not found by the POBSP party, yet because no scientific investigations had been conducted for 80 years, they were counted as part of the atoll flora (Clapp & Sibley, 1971a). Three more visits to Caroline, plus periodic searching by the Falconers, have also failed to uncover most of these ornamentals. Since Caroline’s occasional occupants tended gardens (Lucett, 1851), it is evident that many introduced plants have died out, lacking constant care.

Vascular Plants of Caroline Atoll

Plant Collections: To avoid duplicating Long’s plant collection (Clapp & Sibley, 1971a), we collected only 5 specimens in 1988 and 33 in 1990. Dr. D. Herbst assisted with identification, prepared and deposited the specimens with Long’s in the Bernice P. Bishop Museum, Honolulu, Hawaii, with duplicates in the U.S. National Museum, Washington, D.C. Collection numbers preceded by ‘K’ were collected by A. Kay Kepler; those preceded by ‘L’ are those of the late C. R. Long. Earlier collections of Bennett in 1835 (Bennett, 1840) and Dixon in 1883 (in Trelease, 1884) are noted by date only.

Working with Long’s location records for some species has proven difficult. He was working with an incorrect map (Fig. 7), which showed only 25 islets instead of 39. Much of his work was done at night, which in some places would have made it hard for him to determine his exact location. His references to South, Long, and Nake are undoubtedly correct, and presumably the following: “second islet south of Long” = Crescent; “islet northeast of South Island” = Tridaena; and “fourth islet north of Bird Islet” = Emerald. Long records *Pandanus* on the “second islet south of Nake Island,” which

lacked *Pandanus* when we surveyed the island. Moreover, the first islet south of Nake supports an extensive grove of large *Pandanus* trees on its eastern (lagoon) shore, and we feel confident in ascribing Long's specimen to this island, which we had named "Pandanus" because of this grove. To be consistent, we have ascribed all his other "second islet" specimens to Pandanus Islet as well and assume he made no collections on the actual second islet (Danger).

Species Lists, Annotated Checklist, and Maps of Terrestrial Vascular Plants: Following recent authors Sachet & Fosberg, 1983; Lamberson, 1987), we do not consider Caroline's transient or extinct vascular flora (Table 1) or the vegetables and ornamentals in the Falconer's garden as part of Caroline's viable flora. Table 2 summarizes the current flora, detailing the relative abundance of each species within each plant community. These tables are based on sight records supplemented by all collections, past and present. No beach drift seeds are known from Caroline apart from those species already represented. English and Gilbertese names in Tables 1 and 2 are from Thaman (1987), St. John (1973), and Perry & Garnett (n.d.). If no common name is available, the Hawaiian name, familiar to many students of Pacific botany, is used.

One new species record for the atoll, as yet unidentified, is called Species A (K-90-23, 24): a single sterile shrub 2.5 m high, collected from southwest Motu Mannikiba in coarse strand rubble, is similar to *Clerodendrum inerme*, with leathery leaves and arching stems 4–5 m long. It was found by John Phillips.

Table 3 lists the distribution and abundance of plant species (with subdivisions into tree, shrub, and herb components) on all motus. Figures 11–25 map the entire atoll distribution of each species according to data from transects and aerial maps.

Families are arranged phylogenetically, according to Fosberg & Sachet (1987), with species arranged alphabetically within each family. The taxonomy of vascular plants follows W. Wagner *et al.* (1990), and ferns follow H. Wagner (personal communication). "c% cover" means the percentage of the ground area covered by a particular plant species. In all text and tables, the following symbols apply:

- New record for Caroline
- * Indigenous—plants native to Caroline but also occurring elsewhere (I)
- ** Aboriginal introduction—useful plants brought by Polynesians in pre-historical times (AI)
- # Recent introduction—plants of accidental or deliberate introduction after Western discovery of the atoll (RI)
- A Abundant—generally the major or dominant species in a given area
- VC Very common—often seen but not quite as abundantly as above
- C Common—generally distributed throughout a given area in large numbers
- UC Uncommon—observed uncommonly but more than 10 times in a given area
- O Occasional—here and there, often widely scattered but not forming a major component of the vegetation
- R Rare—observed 2–10 times in a given area
- S Single—only one specimen observed

L Local—found only or principally in one or more restricted areas

D Drift seedling—plant derived from a water-borne seed
+ Not seen 1988–1990 but probably still present

PSILOACEAE

* *Psilotum nudum* (L.) Beauv (Fig. 11)

Formerly Known Distribution: L-3233 from Nake.

Present Distribution: Cosmopolitan, common on remote islands, rare on Caroline. K-90-15 from South. In 1965, common on wet base of *Cocos* only on Nake Island. In 1988 and 1990, a few clumps found similarly on South Island in shady, damp locations, close to lagoon, northwest sector. *Cocos* canopy was 18 m.

POLYPODIACEAE

* *Phymatosorus scolopendria* (Burm. f.) Pichi-Sermolli (Fig. 12; Pl. 34)

Phymatodes scolopendria (Burm. f.) Ching

Polypodium phymatodes L.

Polypodium scolopendrium Burm. f.

Microsorium scolopendria (Burm.) Pichi-Sermolli

Formerly Known Distribution: Recorded 1840, collected 1884; L-3244, L-3250, L-3287 from Nake, Long, and South Islands.

Present Distribution: Range extension from 3 to 11 motus. Rarely a continuous ground cover, usually locally rare to abundant. Commonest on Nake, with cover 10–80%. Well represented on South, especially in open areas of the interior, where soils are moister. On other motus local distribution varied from less than 1 to 80%; accurate mapping is difficult. Absent from motus less than 0.6 ha in size, where habitats cannot provide cover, moisture, and substrate for both sporophyte and gametophyte generations.

Ecology: Hardy. Leaves burn in sun but can withstand very dry conditions. Primarily in *Tournefortia* scrub, mixed forests with *Pisonia* and *Pandanus*, or *Cocos* plantations. Associated with *Cordia*, *Morinda*, *Suriana*. In open clearings within dying *Cocos* forests, occurs in dense mats intermingled with *Boerhavia*, *Ipomoea*, and *Portulaca*. Sometimes gathers in thick bands at the interface of *Tournefortia* and *Pisonia* forests. Prefers shelter, high humidity, "soil," and relative lack of wind, but absent from deeply shaded forests. Rhizomes never exposed on ground surface or epiphytic on trunks, as in wetter islands such as Hawaii or Samoa (personal observation) or in the moister Line Islands (Wester, 1985), indicating that Caroline's habitats are suboptimal. Although most ferns are not halophytic, this species grew (rather stunted) in 1988 amongst sparse herb mats (1% cover) on older beach sands of an ancient reef channel on Long Island (Tr. C), where rainfall provides the sole fresh water, but was (temporarily?) obliterated in February 1990. Rare to uncommon in outer beach strand, and beach scrub with *Suriana* on South, Arundel, and Shark.

Substrata: Dry coral rubble, sand and gravel, rubble with sparse humus, lagoon mud, relatively fertile humus, older beach sands.

PANDANACEAE

* **? *Pandanus tectorius* Park. (Fig. 11; Pls. 35–38,50)

Formerly Known Distribution: Recorded 1840, unidentified *Pandanus*; L-3227, Pandanus Islet, seen on Nake by Long.

Present Distribution: A minor plant community (Plant and Communities section), *Pandanus* is primarily associated with *Tournefortia* or *Pisonia* on the leeward motus. Most common on Nake, with *Cocos* and *Ipomoea*. Range extension from two to seven motus.

Phenology: Flowers and fruit in October, March, and May.

Substrata: Variable. Prefers lagoon mud, pure sand, and rubble–humus, but survives in almost pure rubble.

GRAMINAE

* +? *Digitaria* species

Collected 1883 and recorded as ?*Panicum* (*Digitaria*) *marginata*. Examined by Long, who believes it a *Digitaria* identical to his L-3235. Not found by the authors.

* *Lepturus repens* (Forst. f.) R. Br. (Fig. 13; Pl. 2a)

Formerly Known Distribution: Collected 1883; L-3211, 3221, 3236, 3238, 3247, 3259, 3286 from Windward, Tridacna, Nake, Long, Emerald, Crab, and South Islands, respectively.

Present Distribution: On most dry Pacific atolls. K-88-4, 5; K-90-1, 2, 19 to 21, 25 from South, Tridacna, and Ana-Ana. On Caroline, range extension from 6 to 26 motus.

Ecology: Patchy, rare to locally common. Usually in exposed herb mats with *Heliotropium*, *Laportea*, *Portulaca*, and low *Tournefortia* scrub. Abundance 1–5% cover where not in thick patches. Occasionally inland under *Tournefortia*, *Cordia*, or *Cocos*, fitting the generalization that *Lepturus*, though a pioneer, will often persist as undergrowth in forests. Tufts tiny (few centimeters), dry and scrappy in exposed areas, but to 3 dm where shaded. Never in tall, upright clumps, or with the same abundance as on the drier, filled-in equatorial atolls or islands with sandier habitats (Christopherson, 1927; Fosberg, 1953, personal observation). Never forms a turf.

Substrata: Able to survive in coral rubble of varying coarseness, down to high water mark, but preferred habitat is part sand. L-3286 was from “numerous clumps under *Suriana* scrub on South Island,” perhaps the low, sandy portion of the northwest point (Pl. 45), our best *Lepturus* site. Comparison of Arundel’s chart (1883), recent aerial surveys, and earlier photographs indicate that several motus have altered shape since 1883. The amount of open area on South Island has also decreased markedly since 1883. The distribution of *Lepturus* parallels these changes; there is clearly much less on South Island, and more in newly-created islet fringes.

Since 1965 the lagoon shore of South Island has become overgrown by *Cocos*, so much that both *Suriana* and *Lepturus* are much less common than previously (Pls. 39,40). However, sand and debris will always be shifting, so that *Lepturus* will move from place to place, establishing wherever conditions permit. In the second situation, a comparison of Pls. 2a and 24

from 1883 and 1988, respectively, shows that a century ago the lagoon-facing shores of South Island were far more open than the dense *Cocos* plantations of today. The clumped grass in the foreground of Pl. 2a is undoubtedly *Lepturus*, probably mixed with introduced grasses not seen since that time (*Eleusine indica*, *Eragrostis plumosa*) and the dubious *Digitaria* sp., above.

PALMAE

**# *Cocos nucifera* L. (Figs. 14,36,51; Pls. 2,6,18,24,34,37,44)

Formerly Known Distribution: Recorded 1840, 1884; L-3285 from South Island, extensive groves on South and Nake, scattered on north portion of Long.

Present Distribution: Range extension from 3 to 15 motus. Planted groves on South, Nake, and Long; the rest derived from drift.

Phenology: Flowers and fruit year round.

Ecology: Forms a major vegetation type (Plant Communities section). Primarily South and Nake, where closed canopy forests average 21 m high.

TACCACEAE

**? *Tacca leontopetaloides* (L.) O. Kuntze (Fig. 11)

Tacca pinnatifida Forster

Formerly Known Distribution: Normally an aboriginal introduction on Pacific islands, but on Caroline is first mentioned as planted in 1834 (Bennett, 1840); L-3213 and 3219, and K-90-7 and 90-16 from moist muck, South Island. L-3234, common under *Cocos* and numerous patches found in muck, south end, Nake.

Present Distribution: Common in northwest South. None in flower; each plant had two to three leaves, possibly dying back. None found on Nake, despite searching the south end. Has large underground tubers, dies back, and though cultivated, still occurs spontaneously in *Cocos* groves on many atolls. Currently harvested by the Falconers.

Ecology: Needs fine, moist soil and shade. Though its seeds float for months (Guppy, 1906), it will probably not become established on any other motu, due to the prevalence of rubbly substrates.

Phenology: Flowers and fruit in March and May, dies back in October.

URTICACEAE

* *Laportea ruderalis* (Forst. f) Chew (Fig. 15)

Fleurya ruderalis (Forst. f.) Gaud. ex Wedd

Formerly Known Distribution: Reported 1840, collected 1884. L-3215 common in shady areas South Island; L-3229 scattered on exposed coral and sand, west side Crescent Islet. L-3253 under shade of *Cocos* and *Pisonia* on north side of Long Island.

Distribution and Abundance: K-88-3 South Island, Tr. 1, elevation 0.3 m, under old *Cocos* plantation, in humus and rubble. Range extension from 3 to 32 islets (Table 3). Commonest and most widespread ground cover,

patchily distributed. Rare to locally abundant, percentage cover from less than 1% in herb mats of tiny motus to 60% in tall *Pisonia* forest. Best represented on Nake, Long, Brothers, South, *Pisonia*, Eitei, and Mannikiba, where coverage exceeded 50% in appropriate habitats. To 1.1 m tall on Kimoa.

Ecology: Largest specimens found under *Tournefortia*, *Pisonia*, *Cocos*, or *Pandanus*. Tiny (1–2 cm) and tougher in sunny, exposed sites. Halophytic, pioneering in herb mats on islets less than 0.75 ha in size (e.g., Fishball). Optimum habitat is *Tournefortia* scrub, in sunny clearings, or belts behind beach scrub. Uncommon in *Pisonia* forest. Occurs in both windward and leeward sites, but in greater density leeward. Will persist through several stages of plant succession if given adequate shade.

Phenology: Flowers and fruit in October, March, and May.

Substrata: Primarily beach gravel or coarse rubble. Also rubble–sand mixtures; not lagoon silt.

OLACACEAE

° * (#?) *Ximenia americana* L. (Fig. 11)

Never previously collected. K-90-170 South Island, 50–100 m north of cistern, elevation 0.3 m, 10–20 m from coastal *Tournefortia* fringe, within *Cocos* plantation. Collected by crew of the yacht *Amanita* and posted by Anne Falconer to AKK.

Distribution and Abundance: Locally abundant in one location, about 50 bushes (3–4 m high, 2–3 m wide) spread over about 100 m. Adjacent to indigenous scrub, on edge of *Cocos* plantation near old settlement.

Phenology: Flowering in July 1990.

AMARANTHACEAE

° * *Achyranthes canescens* R. Br. (Fig. 16, Pl. 41)

Never previously collected. K-88-1 South Island, Tr. 5, to 0.7 m, elevation 0.3 m, in *Tournefortia* fringe, coral rubble.

Distribution and Abundance: Quite widespread, primarily in interior scrub and forest of 19 motus (Table 3), from tiny, barely vegetated Fishball (0.73 ha) to the largest, South (106 ha). Density variable: from less than 1% in *Tournefortia* scrub to 50% local ground cover in mixed *Pandanus* forest. Primarily associated with *Tournefortia*. May be locally abundant in clearings in *Pisonia* forests, pure or mixed. Often in a zone dividing *Tournefortia* and *Pisonia* trees, especially on Pig, Brothers, and Nake.

Ecology: Never in natural herb mats. Needs shade but requires some direct sun; rare in pure stands of *Cocos* and *Pisonia*. Prefers small, sunny openings in forest or scrub. Drought-resistant and probably partly halophytic. Dies back annually in the dry season and reappears with winter rains (Anne Falconer, personal communication). To 1.5 m tall. Little or no capacity for dispersal by sea. On other islands, seeds carried by birds, especially fruit pigeons (Guppy, 1906).

but pigeons are absent from the Line Islands. Perhaps dispersed by the long-tailed cuckoo (Ellis *et al.*, 1990).

Phenology: Flowers and fruit present in October, March, and May.

Substrata: Lushest growth in humus soils of forest interiors. Often grows in pure rubble.

NYCTAGINACEAE

* *Boerhavia repens* L. (Fig. 17, Pl. 34)

Boerhavia diffusa L.

Boerhavia hirsuta: Ssensu Bennett, 1840

Boerhavia species: Dixon, 1884

Formerly Known Distribution: Reported 1840, collected 1884; L-3210, 3324, 3239, 3225, 3252, 3262, 3289, 3291 from Windward, Tridacna, Nake, Long, Emerald, and South, respectively.

Present Distribution: Cosmopolitan, widespread in the Pacific. K-90-164 and 165 from Ana-Ana. Range extension on Caroline from 6 to 33 motus (Table 3).

Abundance: Present in every habitat, leeward and windward, ranging from less than 1 to 80% cover. Often in unpredictable patches. Best locations (>50% cover) on Nake, Long, Windward, Pig, Brothers, Arundel, Tridacna, South, Ana-Ana, *Pisonia*, and *Pandanus* Islets.

Ecology: Mostly found beneath *Tournefortia*, either in pure scrub or mixed with *Pisonia*, *Cordia*, *Morinda*, *Suriana*, or *Cocos*. Not in deep *Pisonia* shade; rarely in herb mats. Thick ground cover in indigenous scrub (Shark) or within clearings in old *Cocos*–*Ipomoea* forest (South), where it mingles with *Phymatosorus*, reaching a high density (Pl. 34) and large size (rooting at nodes, vines exceeded 1 m long). BIRDS: Bristle-thighed curlews fed within the *Boerhavia* mat in old *Cocos* forests, South. Sticky seeds (.32 cm [one-eighth inch] long) found entangled in preened down and adhering to contour feathers of a juvenile great frigatebird (Pl. 42). Species is customarily dispersed around large oceanic areas and within atolls by seabirds such as red-footed boobies (Guppy, 1906; Ridley, 1930).

Phenology: Small mauve flowers and seeds present in October, March, and May.

Substrata: Coral rubble with sand or humus, rarely pure beach rubble. Lushest growth in humus-and-guano-laden rubble clearings where *Pisonia* forest once grew.

* *Pisonia grandis* R. Br. (Fig. 18; Pl. 43)

Formerly Known Distribution: Collected 1884; L-3280 4 m tree, north shore, South. Small grove, north end, Long.

Present Distribution: Cosmopolitan, pan-Pacific. Caroline range extension from 2 to 29 motus (Table 3).

Abundance: A major plant community (see Plant Communities section). Caroline's *Pisonia* forests, some of the last remaining groves in the Pacific, are of special conservation value.

Substrata: Occupies, and contributes to, best soils on atoll: mixture of rubble, humus, and guano.

PORTULACACEAE

* *Portulaca lutea* Solander ex Forster F. (Fig. 19; Pls. 34,38)

Formerly Known Distribution: Reported 1840 and 1884; L-3233 and 3292, 3231, 3237, 3255, 3257, from South, Pandanus, Nake, Long, and Emerald, respectively, in open coral, rubble, gravel, and exposed areas, to 1.5 dm high.

Present Distribution: Range extension from 5 to 33 islets (Table 3).

Abundance: Along with *Heliotropium anomalum* is a component of the plant community, Natural Herb Mat (see Plant Communities section). Widespread, predictable on coast and former reef channels but local inland. Covered from one to 60% of land area on almost every transect, windward and leeward, especially facing lagoon. Best areas are Long, Tr. 4 (36-m wide meadow); South, north end of Tr. 6 (50 m wide); Brothers, lee, almost pure mat covering 20% ground (6 m wide); Kimoa, north side (8 m wide), 10 cm high; Eitei, north side, 5 cm high.

Ecology: Primarily occurs along edges of motus in rubble mat and open *Tournefortia* scrub, averages 12 cm high. Prominent in sparsely vegetated areas, extending seaward to high tide level. Halophytic; highly tolerant of sun. A flat mat in exposed areas but lush in inland, rising to 2 dm tall. Generally found with *Heliotropium*, *Lepturus*, *Boerhavia*, or *Laportea*, but may form pure mats. Uncommon in *Tournefortia* scrub, patchy in clearings within *Pisonia* forests up to 13 m high. Exceptionally common in old *Cocos* groves with *Boerhavia*, et cetera (Pl. 34); otherwise rare or absent from closed canopy *Cocos* plantations. Pinker stems found in sunny sites. BIRDS: Provides nesting cushion for masked booby, sooty tern, brown noddy. On noddy rock, brown noddies nest on a thick mat of pure *Portulaca*. Feeding location for shorebirds.

Phenology: Flowers and fruit October, March, and May.

Substrata: Coral rubble and gravel, fine to very coarse. Healthier on older sands and coral-humus.

ZYGOPHYLLACEAE

* *Tribulus cistoides* L. (Fig. 11)

Formerly Known Distribution: Collected 1884. L-3245 in open sandy area among *Tournefortia* shrubs, Long Island. Not seen elsewhere on atoll.

Present Distribution: Not seen on our surveys, but present in 2 sites on west-central Long Island. K-90-161 (collected by Anne Falconer), probably from one of same sites as 1965 collection. Flowers in March.

SURIANACEAE

* *Suriana maritima* L. (Fig. 20; Pls. 6,21,39,40,44)

Formerly Known Distribution: Collected 1884. L-3220, shrub to 1.8 m, east edge of Tridacna Islet.

Present Distribution: K-90-5, 6 from South Island. Range expansion from one to 9 motus (Table 3).

Abundance: Occasional on Caroline. Forms a vegetation unit, Beach Scrub with *Suriana* (see Plant Communities section).

Phenology: Flowers in March and May.

Substrata: Best sites in sand but also on coral rubble.

EUPHORBIACEAE

Phyllanthus amarus Schum. and Thonn. (Fig. 11)

Formerly Known Distribution: Collected 1884. L-3283, herb *Phyllanthus niruri* L. (Trelease, 1884) to 4 dm, common on north side of South Island.

Present Distribution: K-90-10-13, herb, 2 small patches, South Island. Limited to a few square meters in the atoll's only weedy area, less than 10 m² in two small clearings by the recently-renovated cistern, South. A fairly common weed in the Society and Tuamotu Islands, therefore probably arrived with Tahitian copra-cutters and perhaps again within the last 2 years. Caroline's only established "weed" (excluding Polynesian introductions such as *Cocos*).

MALVACEAE

° * (**?) (#?) *Hibiscus tiliaceus* L. (Fig. 11)

Never previously collected. K-90-8, 90-9 from South Island, northwest peninsula, in *Cocos* plantation near old settlement and "landing," in coral rubble and humus, 0.6 m in elevation.

Present Distribution: Two or three large spreading trees in heavy *Cocos* shade, 10 m tall, with recumbent branches forming an impenetrable thicket. This species, culturally important to Polynesians, is either indigenous, an early Polynesian introduction, or an ornamental brought by 19th century settlers.

° * (**?) (#?) *Thespesia populnea* (L.) Soland. ex Correa (Fig. 11)

Never previously collected. K-90-22, 154, 155 from South Island, in *Cocos* plantation and in lagoon strand, northwest peninsula, near "landing."

Present Distribution: Two trees (10 m tall), one near the cistern, the other in a fringe of native vegetation bordering the lagoon. The history of this species is probably the same as *Hibiscus tiliaceus* (above).

* *Sida fallax* Walp. (Fig. 11)

Formerly Known Distribution: Collected by Dixon, 1884, who found one specimen.

Present Distribution: Not seen for 106 years. K-90-156, 157, 158 from South Island, at edge of cistern, north side. One clump located in a sunny clearing, recently enlarged by the Falconers.

CONVULVULACEAE

* *Ipomoea macrantha* R & S (Fig. 21; Pls. 34,37)

Ipomoea tuba (Schlecht.) G. Don

Formerly Known Distribution: L-3228 and 3293, 3242, 3251 on South, Nake, and Long, respectively. Trailing vines, white flowers, stems to 25 m long climbing over *Tournefortia*, *Morinda*, and *Cocos*.

History: Not collected last century, though plantation records indicate that it was a major reason for the abandonments of the coconut plantations: "The Pohue Vine [misidentified as *Tiumfetta* (= *Triumfetta*) *procumbens*], which is the worst pest on the island, was reported in 1921 to be under control" (Young, ca. 1922). Today it still causes severe damage to *Cocos* on South Island, strangling about two-thirds of the plantation (54 ha).

Present Distribution: Range extension from three to seven motus, five Windward and two Southern Leeward Islets (Table 3).

Abundance: Forms part of a vegetation subunit, Dying *Cocos-Ipomoea* Forest (Pl. 34, Plant Communities section). An indigenous, nonparasitic vine, becoming abundant and strangling in disturbed areas. Rampant growth over most of the interior of South Island, where it forms dense tangles up to 25 m high. Less dense thickets on southern *Nake* drape *Pandanus*, *Tournefortia*, *Morinda*, and *Cocos* to 10 m. Our transects on *Nake* were not rerouted or abandoned, as on South. Coverage scant elsewhere, generally 2–5%, except in two *Pisonia* sites, where its coverage was 20% (Long Island, Tr. B; Windward Islet, Tr. I).

Ecology: Lush in dying *Cocos* forests and mixed forest with *Pandanus*, because of relatively fertile soils, moisture, humidity, and partly sunny clearings. Strangles all but the tallest *Pisonia* and *Cordia*. Typically sea-dispersed to atolls (seeds germinate after floating up to 1 year in seawater), crawls inland, progressively dropping seeds, to attain full size in interior forests (Guppy, 1906; Ridley, 1930). Seeds of *I. pes-caprae* are known to be ingested by white terns in the Marshall Islands, perhaps as gizzard stones (Fosberg, 1953). Possibly these same terns, abundant at Caroline, once aided the seed dispersal of *I. macrantha*. Also characteristic of *Cocos* plantations elsewhere in the Pacific (Fosberg, 1965; Stoddart & Sachet, 1969; Lamberson, 1987).

Substrata: Prefers humus-laden rubble but can grow in coarse rubble and sand, especially in leeward areas.

BORAGINACEAE

* *Cordia subcordata* Lam. (Fig. 22; Pl. 27)

Formerly Known Distribution: Collected in 1884, L-3213 and 3261a, 3228, 3246, and 3261b on South, *Pandanus*, Long, and Emerald, respectively; flowering trees to 4.5 m high in leeward coral rubble or along lagoon.

Present Distribution: Africa to Polynesia. K-90-3 from South Island, lagoon edge. Range expansion on Caroline from 5 to 23 motus (Table 3).

Phenology: Peak flowering November through April. Fruits collected in March and May.

Abundance: A separate, though minor, plant community (Plant Communities section). Caroline's *Cordia* forests, typically small and mixed with other emergents, are some of the last remaining groves in the Pacific and are thus of particular importance to conservation.

* *Heliotropium anomalum* H. & A. (Fig. 23; Pls. 17, 33, 45–47)

Formerly Known Distribution: Recorded (as *H. curassavicum*) in 1840, collected in 1884, L-3222 and 3288, 3240, 3248, 3256, 3288 on South, Danger, Long, and Emerald, respectively.

Present Distribution: Pantropical. K-90-17 from Ana-*Ana*. In coral gravel, leeward, and windward shores. Range extension on Caroline from 4 to 34 motus (Table 3).

Abundance: Forms part of a major vegetation unit, Natural Herb Mat (Plant Communities section), often associated with *Laportea*, *Lepturus*, or *Boerhavia*. Area coverage ranges from less than 1% to 50%. Widespread, predictable on wind- and salt-blown, low flats where vegetation does not overhang edge of motu. Also in ancient reef channels and newly evolving land connecting islets. Covers major areas of islets—that is, those less than 1.0 ha (e.g., Fishball, Skull, and Bo'sun Bird). Best developed on Skull, Tridacna, South, Emerald, and Mannikiba (50% coverage, western seaward rim).

Ecology: Halophytic pioneer. Heights to 22 cm, averaging 7 cm. Thrives in heat and exposure.

Phenology: Flowers and fruits year round.

Substrata: Primarily coral rubble and rubbly sand. Marginal habitats extend down to high tide line in areas of coarse coral chunks, where it is tiny and leathery.

* *Tournefortia argentea* L. (Fig. 24; Pls. 8, 37, 47, 48)

Messerschmidia argentea (L.f.) Johnston

Formerly Known Distribution: Collected 1884, L-3216, 3226, 3241, 3249, 3258 from South, Tridacna, *Nake*, Long, and Emerald Isle; shrub to 3 m high, edge of lagoon and above high tide, with white flowers.

Present Distribution: Range extension from 5 to 38 motus (Table 3). Widespread in the Pacific, especially on small islets. Caroline's large tracts are excellent examples of relatively undisturbed, pure *Tournefortia* scrub and forest.

Abundance: Dominates the atoll woodlands, forming the major vegetation type (Plant Communities section). On almost every motu ranging from a spattering of exposed shrubs within herb mats, through scrublands and taller forests to 14 m high.

Ecology: Supports seven species of breeding seabirds; provides feeding habitats for reef herons (*Egretta sacra*), shorebirds, land crabs, and rats.

Phenology: Flowers and fruits year round.

Substrata: Pure coral clinker; mixtures of rubble, gravel, sand, and humus.

BRASSICACEAE

* *Lepidium bidentatum* Montin (Fig. 11)

Formerly Known Distribution: Reported in 1825: "a boat load of pepper-grass and pursley" (Paulding, 1831) and in 1835, "a *Lepidium* of luxuriant growth" (Bennett, 1840). Collected by Dixon as *L. piscidium* Forst in 1883.

Present Distribution: Widely distributed throughout the North and South Pacific. K-90-169 and 171 (collected by

Alexandre Falconer), on *Tridacna* and *Pisonia*, most probably in coastal *Tournefortia* scrub.

RUBIACEAE

* *Morinda citrifolia* L. (Fig. 25; Pl. 48)

Formerly Known Distribution: Reported 1840, collected 1884. L-3214, 3217 and 3282; 3232; 3254 on South, Nake, and Long, respectively.

Present Distribution: K-90-4, 18 from South Island, lagoon edge, and Ana-Ana, respectively. Range extension on Caroline from 3 to 30 motus (Table 3).

Abundance: Coverage from 2% to 50%. Basically an inland species, widespread and predictable in scrub and forest understory. Rarely a component of the canopy, except on Raurau, where *Morinda* grows 12 m tall in a 13 m *Pisonia* forest. Essentially associated with established *Tournefortia* woodlands on motus greater than one hectare in size. Quite common on South Island despite major disturbance, occurring within beach strand, *Cocos* plantations, and *Cocos-Ipomoea* interior. Best locations (40–60% coverage): Nake, Tr. 3; *Tridacna*, both transects; Long, Tr. 8; Raurau and Ana-Ana.

Ecology: Appears early in plant succession: in *Tournefortia* scrub as an early pioneer (Stage I), then from Stages II to IV, progressively becoming more common and robust. Not in pure *Pisonia* forest (Stage V). Much less common in *Pandanus* stands. Although it thrives best in light to heavy shade, preferably growing in moist “soil,” one leathery seedling (7 cm high) had gained a foothold in exposed rubbly *Heliotropium* flats on Fishball Islet.

Biogeographical Note: Generally considered a naturalized aboriginal introduction on most Pacific islands, *Morinda* could be native to Caroline, as theorized for the northern Line Islands (Wester, 1985). Although possibly introduced by early Tuamotuan settlers, its present distribution strongly suggests that it is indigenous. Throughout the atoll *Morinda* occurs in the greatest densities on motus with no anthropogenic forests or in areas distant from historical settlements (Fig. 26). On Nake, *Morinda* occurs frequently—in places abundantly—within the interior *Pisonia* forests, yet its coverage is only 5–10% in mixed *Pandanus*–*Cocos* forests in the southern sector. It also appears to be part of natural biological succession (Table 6). Further support for this theory comes from nearby Flint. Though there is no direct archaeological evidence that Flint was settled in prehistoric times (Garnett, 1983), our 1990 surveys found *Morinda* in all habitats (mixed woodland, native coastal scrub, *Cocos* plantations, and abandoned settlement).

Originating in Polynesia, *Morinda* has been widely dispersed by man but has apparently also spread, unaided by man, “widely by sea in the Malayan and Polynesian Islands” (Ridley, 1930). Its air-filled, buoyant pyrenes can float for at least 53 days and “its seeds are almost certainly disseminated by birds and bats” (Guppy, 1906). It could also be disseminated by *Coenobita* crabs and rats within and between motus, as has been found elsewhere by Ridley.

Phenology: Flowers and fruits year round.

Substrata: Coral rubble, gravel, sand, and humus. Rarely found in coarse clinker. On larger motus, prefers moist soils under tall forests.

GOODENIACEAE

° * *Scaevola sericea* var. *sericea* Vahl (Fig. 11)

Scaevola taccada var. *sericea* (Vahl) St. John

Never previously collected. K-88-2, Windward Islet, central-windward side, elevation 0.3 m.

Distribution and Abundance: One wind- and salt-sheared “hedge,” found by K. Teeb’aki on Windward Islet, was growing on a coarse rubble beach. “The saltbush..., being recorded for the first time too from the island...covered approximately 3% of the islet’s land area [this probably can be translated as “3% of the area covered at that location on the transect,” as we understood from Mr. Teeb’aki’s description that it was quite small], occupying the mid-windward side. The patch grew very low—only up to 2’ high with its foliage forming an extended raised mat canopy all along the area it occupied” (Teeb’aki, 1988). We have been unable to return to this spot to observe and photograph it directly.

Because *Scaevola* is hardy, halophytic, and widespread in the Pacific, it is surprising that it is so rare on Caroline. However, none occur on Vostok, and only one clump is known from Flint (Clapp & Sibley, 1971b; Garnett, 1983). Fosberg (1953) noted that *Scaevola* seeds are transported by bristle-thighed curlews (*Numenius taitensis*) in the Marshall Islands: curlews are common on Caroline (Subchapter 1.2, this volume) and could have brought seeds from elsewhere.

Substrata: Coarse rubble, windward beach.

° * *Scaevola sericea* var. *tuamotensis* (St. John) Fosb. (Fig. 11)

Scaevola taccada tuamotensis St. John

Never previously collected. K-90-168 (collected by Alexandre Falconer), northeast peninsula, South Island, in coral rubble.

Present Distribution: One individual, of unknown size, with *Suriana* and *Heliotropium*, northeast peninsula, South Island, facing the inner side of the “blind passage.”

Floristics and Ecology of the Motus

Size of the Flora: Atoll floras characteristically lack diversity. Numbers of species range from 3 to around 150 in the Pacific and 284 in the Indian Ocean. The flora of the Southern Line Islands is particularly impoverished because of 1. their easterly location (far from the major source areas of Australasia); 2. low profiles (most only rise a few meters above sea level); 3. lack of topographic diversity (most have a very limited range of habitats); 4. low to medium rainfall (approximately 1,500 mm p.a.); and 5. edaphic factors such as salinity, highly calcareous soils, etcetera. Long-distance dispersal and hardiness are important factors in establishing a flora, especially since the closest high island, Tahiti, is 830 km away, and the ultimate source of its flora, the Malayan–Melanesian region, is over 8,000 km away. South America, the closest continent, is

approximately 9,000 km distant. The motus of Aitutaki, for example, at a similar latitude but further west and wetter, are considered depleted with 45 species. Fanning, at a similar longitude but wetter, has 123 species. Tarawa, 3,900 km to the northwest, receives a similar rainfall but supports 109 species.

Where an atoll's potential flora is larger, the increased shade and greater protection from wind, salt spray, and storms result in a greater number of natural plant species on its larger motus. However, such atolls are generally inhabited and alterations by both aboriginal and modern man have modified their original flora. Caroline's isolation, variety of islet areas, and minimal human disturbance all contribute to its excellence for the study of atoll evolution.

The number of species presently established on Caroline's 39 motus is 27 (Tables 2, 3). The previous expedition in 1965 (Clapp & Sibley, 1971a) collected 20 species, of which 4 were new to the atoll. Their total of 35 species, however, incorporating reports and collections from the 1800's, is misleading. Our total, 6 of which were new records, would have brought the atoll total to 44 (plus about 15 more unestablished, mostly garden, plants). However, following recent custom (see Vegetation section), we have listed transient or extinct members of the flora separately (Table 1). To include them would obscure the near-pristine nature of the atoll and bias our analyses of species-area relationships.

The 1883 drawings of the South Island settlement, inhabited when most of Caroline's species were catalogued, shows that the island was vastly different (compare Pls. 2 and 24). A century ago homes were set amidst large grassy clearings; now the site is completely obliterated beneath shady 21-m-tall coconut palms. Nine exotic plant species have not been seen for over a century (Table 1). Evidently most ornamentals and domestic vegetables perished during uninhabited periods. The present residents struggle to keep garden plants alive because of poor soils, irregular rainfall, and foraging land crabs. A few native species might also have been eliminated during the guano and copra-harvesting years.

Numbers of Indigenous Plants: A comparison of the percentage of indigenous species between different island groups (Table 4) shows that Caroline, with 85%* (N = 23) indigenous, is unusually high. Only 11 of 44 Pacific atolls reviewed have more than 75% of their species indigenous. Of these, nine (including Caroline) are remote and lack permanent human occupation.

The Tuamotu Islands (149° to 134°W) lie east and south of Caroline, yet they harbor considerably larger floras. Rainfall is similar. Three of them average 121 species (Table 4), averaging 42 indigenous species. When the variables rainfall and distance from a colonization source to the west are considered, the proximity of the Tuamotus to the diverse high

islands of the Societies seems to play a major part in determining their indigenous flora. A similar situation exists in the southern Cook Islands. Caroline and other remote Line and Phoenix Islands are sufficiently isolated from high volcanic islands that they exhibit a much simpler flora. Tahiti, the closest high island (830 km south), is in the wrong direction for direct currents, winds, or vagrant birds to bring seeds to Caroline.

Composition of the Flora (Tables 2, 3): Caroline's botanical affinities lie with other southern Line Islands and the Tuamotus. Although the strand and inland floras consist of pan-Pacific or pantropical species, there are several widespread species and communities that are notably absent. Those that survive have withstood the atoll tests of time—poor soils, scarcity of fresh water, periodic inundation by salt water, intermittent cyclonic storms and hurricanes, harsh climate, and high seedling mortality. Caroline provides an excellent ecological laboratory in which floristic correlations with variations in habitat, motu size, and leeward/windward aspect may be studied. Fosberg (1985) and Sachet (1967) have noted the importance of such details in understanding the biogeography and taxonomy of Pacific plants.

Caroline's present established flora includes only one weed species (*Phyllanthus amarus*), represented by a tiny patch less than 2 m² in size. There are two Polynesian introductions (*Cocos*, *Tacca*). *Pandanus tectorius*, *Morinda citrifolia*, *Thespesia populnea*, *Ximenia americana*, and *Hibiscus tiliaceus*, though indigenous, may have been introduced by Polynesians or 19th-century settlers. (See section on Vegetation.)

Trees: Seven species present. Only three—Pacificwide natives—are widespread: *Pisonia grandis*, *Morinda citrifolia*, and *Cordia subcordata*. Two are locally abundant: *Cocos nucifera* and *Pandanus tectorius*, while the rest, *Thespesia populnea* and *Hibiscus tiliaceus*, are rare and limited to the old settlement site. The absence of typical Pacific species such as *Calophyllum inophyllum* and *Guettarda speciosa* is notable, as they occur naturally on atolls such as Rangiroa, further east (Stoddart & Sachet, 1969).

Shrubs: Five species present, at least four indigenous. Only *Tournefortia argentea* is abundant; its most abundant size class is under 4 m. *Scaevola* and *Suriana*, tough and widespread elsewhere, are poorly represented on Caroline. It is noteworthy that two varieties of *Scaevola sericea* are present. Species A is represented by a single individual, *Ximenia americana*, by a single, large patch. *Pemphis acidula*, though common on atolls of similar latitude and climate, is absent from most of the Line and Phoenix groups (Stoddart & Gibbs, 1975; Fosberg & Sachet, no date). This may be due to the paucity of its preferred habitats: low rocky substrates (reef rock, conglomerate rock) and sand-gravel ridges.

Herbs: Fifteen species present, at least 12 indigenous. Of these only seven are common: *Heliotropium anomalum*, *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Achyranthes canescens*, *Lepturus repens*, and *Phymatosorus*

* Note: Perhaps as high as 93%; the *Digitaria* sp., if still extant, is of unknown identity and origin, and Species A has yet to be determined.

scolopendria, *Ipomoeamacrantha* and *Tacca leontopetaloides* are locally abundant, while *Phyllanthus amarus*, *Tribulus cistoides*, *Lepidium bidentatum*, and *Psilotum nudum* are rare and localized. *Digitaria* sp. may be extinct. The fact that *Sida fallax* has only been recorded twice in 106 years is curious.

Ecological Succession

We have attempted to trace the development of Caroline's flora from the smallest to largest motus, using field data and aerial photos, which reveal past geological processes. Three tables provide this analysis of ecological succession: Table 5 presents Caroline's motus in order of ascending size, together with the numbers of plant species and major plant communities. Since the atoll's total land area is small, our data provide relatively complete floristic lists for each islet and detailed maps of their plant communities (Figs. 37–57). The number of species varied from 3 growing on 4 tiny islets (0.02 ha each) to 23 on South (104.41 ha). Because the total number of species for the entire atoll (27) is also small, the addition of one or two rare species contributes significantly to the total flora. Such additions must be kept in perspective when evaluating plant succession.

Table 3 provides a summary of plant species distribution by islet in decreasing order of abundance, and Table 6 is a summary of plant species distribution and relative abundance with respect to islet area and the primary mode of seed dispersal.

Basic Seral Stages

Islets appear, grow, mature ecologically, or vanish in violent storms. Many interacting factors, including geographical (islet area, atoll shape, distance from high islands and continents), geological (changes in sea level), chemical (nitrates from bird droppings, leaf fall, et cetera), climatological (wind, droughts, storms, microclimates), and biological (seabirds, rats, land crabs, and man, both aboriginal and modern), constantly interact to change conditions. The relative influence of some of these factors is evident when comparing the floras on motus of different sizes.

Seed-dispersal mechanisms (Table 6) and the presence of underground fresh water are also vital. Unfortunately, the relationships between groundwater salinity, species distribution, and vegetation patterns on atolls are poorly understood (Fosberg, 1985). The presence and relative salinity of permanent water depends on Ghyben-Herzberg lenses of varying thickness on different islets, and this in turn depends upon island dimensions (especially width), soil porosity, rainfall, tidal fluctuation, and other hydrological factors. Though groundwater supplies have been studied on many atolls (Wiens, 1962; Maude, 1953), each island group is so unique that it is unwise to extrapolate information from one to the other.

Caroline's 39 motus fall naturally into 4 size classes: motus with areas of a) <0.2 ha, b) 0.2 to 0.7 ha, c) 0.8 to 25.0 ha, and d) >25.0 ha. These size groupings harbor all 5 of the seral stages identified on Enewetak Atoll (Lamberson, 1987), tailored to reflect Caroline's particular geography, geology, and impoverished flora. Each stage may be the sole example of ecological succession on an islet or may occur as

one of several stages. Typically the early stages cover the peripheral rubble and scrubby outer zones, while the later ones appear as a series of roughly concentric bands progressing inland.

Stage I: Early pioneers on sandbars, spits, or small rubbly islets subject to storm damage and washover. Harsh conditions, intense sun, drying winds, salt spray. High salt concentration in the substrate. Lack of fresh water and nutrients. Plant genera present include *Heliotropium*, *Portulaca*, *Lepturus*, *Boerhavia*, and seedling or open *Tournefortia* scrub. No *Cocos*. This stage is found on many small motus (Noddy Rock, Fishball) and former interislet channels (e.g., Long Island).

Stage II: Thick scrub of mixed genera, often impenetrable. Its protective barrier allows for the development of vegetation on the larger islets. Seabirds begin to contribute to the soil (guano, eggs, regurgitated fish, decaying nesting material). Plant genera include *Tournefortia*, *Suriana*, *Cordia*, and *Laportea*. If *Cocos* present, accompanied by coconut crabs. Very common around the periphery of most motus just inland of the native herb mats or flanking sheltered shores adjacent to the lagoon (South, Kota).

Stage III: Trees larger, seabirds add further to soil fertility. Open grassland may develop in sunny clearings (*Tridacna*). Added plant communities and *Cordia*–*Tournefortia*, *Tournefortia*–*Morinda*, and *Pisonia*–*Tournefortia* forests. Occurs in the next inner concentric zone of vegetation to Stage II on larger motus (Nake, Long) or, more commonly, the entire interior of smaller ones (Pandanus, Southern Leeward Islets).

Stage IV: *Pisonia* dominates the older mixed forest. *Morinda* and *Tournefortia* reach for the sun. Forests are more open. Undergrowth mostly a ground cover of *Laportea*, *Boerhavia*, *Lepturus*, and *Portulaca*. Covers the main portion of larger islets. If *Cocos* and *Pandanus* present, forms a mixed forest with vines (southern Nake, Shark). Coconut crabs common. A widespread stage in the center of most motus (Central Leeward, Windward Islets).

Stage V: *Pisonia* takes over. Other trees are confined to the forest edges. Always in the deep interior of the larger islets. Little or no ground cover. Abundant nesting black noddies (*Anous minutus*). A more restricted stage (Brothers, Raurau, central Nake, Pig).

Ecological Succession on Motus of Different Size Classes

To assist discussions of succession on Caroline's motus, refer to the individual vegetation maps and graphs (Figs. 27–57) and photographs (Pls. 13–80), particularly Figs. 27–30. The latter figures summarize the amounts of each islet's surface covered by each major plant community, as well as providing the numbers and percentages of indigenous species for each islet.

a) **Motus with Areas <0.2 ha** (Figs. 27,31; Pl. 49; Tables 5,6): Caroline has four motus in this category, three windward and one leeward, whose combined area totals 0.15 ha. There are also three incipient islets which, because of their temporary character, have not been counted in Caroline's overall total (Fig. 2; Pl. 15). With the exception of Noddy Rock—a jagged, upraised limestone plateau—all consist

predominantly of coarse coral rubble (75–98% coverage). These tiny motus are the simplest ecosystems on the atoll, representing early Stage I in plant succession. The number of plant species per motu averages three, all hardy, sea-dispersed, and salt-tolerant pioneers (*Heliotropium*, *Portulaca*, *Lepturus*, *Tournefortia*). The sole plant community is a natural herb mat of varying thickness and extent. *Tournefortia*, though stunted and scattered, is not sufficiently common to form a separate scrub habitat. Indigenous vegetation covers 2 to 22% of the islet areas. Seabirds, especially brown noddies and red-tailed tropicbirds, may attempt to nest.

b) Motus with Areas 0.2 to 0.7 ha (Figs. 28,31; Tables 5,6): There are five leeward motus in this category whose combined areas total 2.21 ha. Their vegetative cover is more extensive and diverse than in size class a, with herb mats and *Tournefortia* scrub and forest, but open rubble is still abundant (30–55% cover). Plant succession corresponds to late Stage I and Stage II. The average number of species is 8.2 (range 6–11), one-third of Caroline's total. All vegetation on these motus is indigenous except for a few *Cocos* palms. Seeds are dispersed by sea, wind, and birds.

With the appearance of shrubs, the number of species increases markedly, and woodlands, primarily of *Tournefortia*, form and expand to create dense thickets averaging 5 m tall and covering 25% of the land area. Canopies of 10 m occur on motus Nautonga and Kota. Seabird colonies of up to six species (brown and red-footed boobies, great frigatebirds, black and brown noddies, white terns) are present.

A low herb mat, dominated by *Heliotropium*, *Portulaca*, *Boerhavia*, and, more rarely, *Lepturus*, develops first, after which *Tournefortia* quickly becomes established. Shade, producing locally humid conditions, and better "soils" derived from guano, decomposing leaves, and the activities of land crabs and rats, provide appropriate habitat for *Laportea* and occasional *Phymatosorus* and *Achyranthes*. The major tree species—*Pisonia*, *Morinda*, *Cordia*, and *Cocos*—subsequently appear but are relatively rare. *Pisonia*, typically an inland species assumed to need companion trees and underground water (Wiens, 1962; Spicer & Newbery, 1979), could well be salt tolerant as it occurs on motus as small as 0.2 ha (Tables 5,6). In this size class *Pisonia* occupies only 2–6% of the total islet areas.

c) Motus with Areas from 0.8 to 25.0 ha (Figs. 29,31; Tables 5,6): All 27 motus in this category share a similar complement of species and plant communities (Tables 5, 6). Their combined area totals 124.35 ha. They are well wooded (Fig. 29), although the leeward motus have a higher proportion of rubble and herb mats, and forests are higher to windward. Unvegetated rubble covers less land area (21%) than in size classes a and b (87% and 39%, respectively). Within the woodlands of these motus, substrates mature from basic rubble to primitive "soils" with small, but significant, structural development. Their flora shows increasing diversity with size, and almost the full complement of seabirds may nest.

All natural ecosystems are firmly established; canopy heights range from 4 to 21 m. On Booby Islet (0.84 ha), *Pisonia* suddenly becomes very common, and the *Pisonia* forests on North Brothers (1.71 ha) and Pig (7.25 ha), at 21 m, are the

tallest on Caroline. As rich guano and dead foliage accumulate, a layer of phosphate-rich humus enables those species already present but poorly represented on the small motus (*Pisonia*, *Morinda*, *Boerhavia*, *Laportea*, *Achyranthes*) to increase in abundance and stature (Table 6). Additional species are *Suriana*, *Pandanus*, *Scaevola*, *Ipomoea*, *Lepidium*, and Species A.

Plant succession, ranging from Stage III to Stage V in the interior, primarily involves forest maturity rather than the addition of large numbers of species. On the larger islets, the number of plant species increases by relatively small increments, filling out the subcanopy layers and, in the cases of *Cordia* and *Pandanus*, adding variety to the canopy.

The average number of plant species is 11.0, ranging from 4 to 15. If we divide the motus into smaller size classes, we find that their species numbers increase slightly with increasing size: 8.0 species for areas 0.8–1.0 ha, 9.8 species for areas 1.1–2.0 ha, 11.5 species for areas 2.1–4.0 ha, 11.3 species for areas 4.1–10.0 ha, and 12.0 for areas 10.1–22 ha. An increase in herbs (range 3–9) is primarily responsible for these higher averages (Table 5).

Despite the large range of motu sizes in this category, plant communities are essentially natural (Table 5). Their overall species composition is 96% indigenous. Seventeen of the motus lack *Cocos*, the only introduced species in this area category, which is represented by small, isolated clumps or individual palms.

On the larger motus, and within the taller forests, more species of birds, especially red-footed boobies, great frigatebirds, white terns, and black noddies, nest in increasingly large colonies, furnishing more minerals to the developing soils, especially where *Pisonia* covers large areas.

In summary, by the time a motu on Caroline has reached 0.8 ha in size, all the natural plant communities, most species of trees, shrubs, and herbs, and most species of seabirds are present. In Caroline's depauperate flora there are few species left to increase floral diversity on the larger islets, regardless of their size. This is very different from the inhabited atolls such as Kapingamarangi.

Although we do not know when true freshwater lenses develop, they may occur in motus of this size class. If we assume that *Pisonia* is not salt-tolerant, limited fresh water must be available on motus as small as 0.2 ha, and actual freshwater lenses may begin forming at around 0.7 ha, as indicated by the sudden proliferation of *Pisonia* forest (Tables 5,6). However, the Falconers have not been successful in finding any underground fresh water on Motu Ana-Ana (2.16 ha), which suggests that *Pisonia* may be salt-tolerant.

d) Motus with Areas >25.0 ha (Figs. 30,31; Tables 5,6): On Caroline, no motus fall between 22 and 75 ha in size. Thus the three motus in this category (Nake, South, Long) cover a limited range of sizes: 75.98 to 107.50 ha. They average 18.0 plant species. The floral components and forest heights of these larger motus (Figs. 32,33; Table 5) are essentially the same as for class c. There are no additional ecosystems (mangrove swamps, salt flats, grasslands, etcetera) or understory layers. Ten species, all rare or uncommon, are present only on the larger motus (Table 3): *Scaevola*, *Tribulus*, *Hibiscus*, *Thespesia*, *Ximenia*, *Psilotum*, *Tacca* (introduced in 1834),

Phyllanthus, *Sida*, and the dubious *Digitaria*. Four, possibly as many as eight, are indigenous. In 1965, one vine of the indigenous *Ipomoea pes-caprae* was also found, but three subsequent surveys failed to locate it.

Species–Area Relationships

The relationship between the numbers of plant species and island size has long fascinated biologists (Fosberg, 1949; Wiens, 1962; MacArthur & Wilson, 1967; Whitehead & Jones, 1969), yet data from uninhabited islands is scant. The studies from Kapingamarangi (Niering, 1956; Wiens, 1956) and Aitutaki (Stoddart & Gibbs, 1975) treat atolls with long histories of human occupancy. Some of the villages on Kapingamarangi's 23 motus date to 1200 A.D. Aitutaki's 16 uninhabited motus lie adjacent to a westernized volcanic island in an "almost-atoll." People on both these atolls have profoundly influenced their flora.

Caroline provides an opportunity to compare the numbers of species on motus of different sizes in an uninhabited atoll, then to compare the results with Kapingamarangi, Aitutaki, and uninhabited islands in the Line and Phoenix groups that have no introduced species and have experienced minimal human contact.

Comparisons of Species–Area Relationships with Other Atolls: Studies of Kapingamarangi (Niering, 1956) contributed greatly to theories of island biogeography (MacArthur & Wilson, 1967). Because its motus cover the same range of sizes as Caroline, the two atolls might be expected to exhibit similar patterns. However, their species–area relationships are completely different. On Kapingamarangi, islets less than 1.4 ha showed a constant, small number of species, after which islets up to 100 ha showed a direct correlation of area with numbers of species. On Caroline, a motu of 1.4 ha supports almost two-thirds of the total number of species, and plant diversity on islets up to 107 ha shows only a slight, but not necessarily steady, increase (Table 5).

Species–area relationships on the motus of Aitutaki (Stoddart & Gibbs, 1975, Figs. 33 and 34 of that paper) conformed to the Caroline model: the number of species increased only slightly on motus from 4 to 71 ha. Unfortunately, Aitutaki had only one motu less than 1.4 ha, so comparisons for smaller islets cannot be made. The floras of all three atolls have been impacted by man, but Caroline far less so than the others. Much of the floral diversity on larger islets at Kapingamarangi is derived from plants introduced by man and cannot be considered normal. Caroline and Aitutaki provide much better samples of natural plant species–area relations on atolls.

Six islands in the Line and Phoenix groups (Malden, Starbuck, McKean, Phoenix, Vostok, Birnie) are uninhabited. Their flora is entirely native. All are Caroline's "neighbors" in an oceanic sense, and all except Vostok are dry, receiving about 750 mm (30") of rain yearly. They are old, essentially filled-in atolls, containing hypersaline central lagoons or no lagoon at all. Although the largest island (Malden) has the greatest diversity, there is only a very small linear increase in plant species with increasing area (Table 8). Plant diversity is more a function of climate (hot and dry) and distance from source areas, than size, similar to the situation on Caroline.

The Question of Fresh Water: The Kapingamarangi data were analyzed with availability of fresh water in mind (Wiens, 1962; Whitehead & Jones, 1969). These authors suggested that 1.4 ha is the threshold at which a freshwater lens can develop. Below this size only halophytes can survive. They argue that, as there are only a limited number of salt-tolerant species, the floral composition on islets below 1.4 ha is relatively constant. On larger islets, species numbers increase in direct proportion to land area, because permanent groundwater promotes the survival of an increasing variety of nonhalophytic plants.

The groundwater versus plant model does not apply to depauperate Caroline for a number of reasons: first, the number of plant species is not constant on islets below 1.4 ha; in fact, species are added faster on motus from 0.02 to 1.4 ha than any other size range.

Second, on Kapingamarangi, the number of species increased in direct relation to islet size from 1.4 ha to 100 ha. On Caroline, species numbers increased only slightly from 1.4 to 22 ha and exhibited another minor increase from 70 to 108 ha (see Fig. 31; Tables 5,6; and Ecological Succession section). Thus, Caroline's data do not support the area-diversity theory.

Third, Whitehead & Jones (1969) argued that the flora on "small" motus lacking a freshwater lens (i.e., <1.4 ha) consists only of salt-tolerant strand species. This is not true on Caroline (Table 6). In addition to harboring the usual strand species (*Tournefortia*, *Portulaca*, *Laportea*, *Heliotropium*, *Boerhavia*, *Lepturus*), Caroline's "small" motus also support inland species that are generally considered nonhalophytic (*Pisonia*, *Morinda*, *Achyranthes*, *Cordia*, *Phymatosorus*). Either these latter five species are moderately salt tolerant, or on Caroline the minimum islet size with a freshwater lens is much less than 1.4 ha, or both.

Fourth, Whitehead & Jones (1969) postulated that the nonhalophytic species are those that control overall species–area associations. This may be a good generalization for less remote islands but does not hold up for atolls with depauperate floras (Table 6). For example, on Caroline the halophytic *Ipomoea macrantha*, *I. pes-caprae*, *Scaevola sericea*, *Sida fallax*, *Lepidium bidentatum*, *Hibiscus tiliaceus*, *Thespesia populnea*, and *Tribulus cistoides*, which theoretically should only occur as strand species on the smaller islets, occur *only* on larger islets. In addition, several nonhalophytes (e.g., *Morinda*) were found at Caroline on small motus where one might only expect to find strand species.

Fifth, the above authors do not mention bird-dispersal of seeds, which is probably a factor that needs to be taken into account on remote islands: at Caroline, *Pisonia* and *Boerhavia* contribute to the floral diversity of islets from 0.2 ha to 108 ha.

Sixth, Caroline does not have an assemblage of nonstrand plants that *only* occur on larger motus; the only naturally occurring, nonstrand plant is *Psilotum*.

Seventh, the greatest factor complicating our understanding of Kapingamarangi's natural evolutionary processes is the presence of numerous exotics: of its 98 vascular plants, only 38 (39%) are indigenous. Its exotics include numerous weedy herbs and food plants, which occupy gardens, abandoned house sites, taro patches, and plantations (*Cocos*, *Pandanus*, *Artocarpus*). These man-made habitats are particularly

prevalent on larger islands. Such an abundance of exotics, both in species and area covered, renders a discussion of natural processes on Kapingamarangi almost impossible. Undisturbed habitats such as those on most of Caroline's motus, and on other uninhabited Pacific islands whose quota of indigenous plants exceeds 75%, provide far better data on species-area relationships.

Motu Size in Relation to the Distribution of Trees, Shrubs and Herbs: As one progresses from small to large islets (Table 5), the number of tree species rises from 0 to 7, the number of shrubs from 1 to 4, and the number of herbs from 2 to 12. Caroline's trends are similar to those at Aitutaki (Stoddart & Gibbs, 1975), where the numbers of trees and shrubs are relatively constant over a wide range of motu sizes (3.8–71 ha), while the number of herbs shows a slight increase. There are too many recent exotics on Kapingamarangi for comparisons to be valid. We believe that if Niering's data were reanalyzed, using *only* indigenous species, similar generalizations would be found, viz.: most species on atolls establish rapidly on small motus, after which a few additions occur on motus of increasing size until the maximum number of potentially available species is reached. cursory examination of Niering's Fig. 31, detailing the breakdown of total species numbers into indigenous and nonindigenous components, bears out this hypothesis.

Plant Communities

General Account

The total area covered by vegetation on Caroline is 357.55 ha, fully 90% of the combined areas of all the motus. Of this, two-thirds (289.82 ha) is woodland. Substantial areas of Caroline's native woodlands and herb mats are pristine, and 85% (possibly as high as 93%) of its plant species are indigenous. Twenty-three (60%) of its 39 motus harbor wholly indigenous vegetation (Figs. 27–30). Atolls that support substantial areas of native forest are typically remote and uninhabited. Where people are present, native vegetation is usually confined to the smallest motus or the extremities of larger ones—areas with marginal human usefulness.

Typical of atolls, but unusual for the tropics, are monotypic stands of shrubs and trees. Caroline is rich in such woodlands (Figs. 18,22,24,27–30; Table 9). The present vascular flora of Caroline, 27 species, is organized into 7 plant communities (11 subcommunities) defined principally by dominant species (Fosberg, 1953, 1977a). Eight subcommunities are natural, three are anthropogenic (Table 5). The subcommunities include a mix of dominant species, which are discussed in the major Community sections below.

NATURAL COMMUNITIES:

Natural Herb Mat

Tournefortia Scrub and Forest

Beach Scrub with *Suriana*

Cordia Forest

Pandanus Forest

Pisonia Forest

ANTHROPOGENIC COMMUNITY:

Coconut Woodlands

Natural Herb Mat (67.73 ha) (Figs. 19,23; Pls. 20,33, 34,45,46,47)

Widespread and predictable on wind- and salt-blown coastal coral rubble and incipient motus, these mats are composed primarily of *Heliotropium* and *Portulaca*. They are pioneers on newly emergent motus, cover most of the ground area of small motus, extend inland along ancient reef channels, and typify newly evolving land that connects or augments established islets. Natural herb mats may persist through all five stages of plant succession as long as sunny openings occur. Caroline's motus illustrate two general principles: 1. the smaller the area of an islet, the more extreme is the strand character of its vegetation, and its corollary; 2. as islet areas enlarge, strand flora becomes less important (Fosberg, 1949).

The following species are present (see Table 2 for abundance indices):

Trees: *Morinda citrifolia* (one drift seedling on one motu);

Shrubs: *Tournefortia argentea*, *Suriana maritima*, and *Scaevola sericea*; and

Herbs: *Heliotropium anomalum*, *Portulaca lutea*, *Boerhavia repens*, *Lepturus repens*, *Laportea ruderalis*, *Lepidium bidentatum*, and *Ipomoea macrantha*.

Near the high water mark, the herb mats are recumbent, leathery, and somewhat desiccated. As environmental conditions improve further inland, they spread more laterally and average up to 7 cm in height. Their rubbly habitat, often sprinkled with *Tournefortia*, resembles a low savannah. Although these prostrate herbs can tolerate dazzling sunshine, they grow most vigorously when slight shade, and hence a higher relative humidity, is present. Under these conditions they may attain a height of 22 cm and form a fairly thick mat. With too much shade the mats disappear or their species proportions and abundance changes according to the presence or absence of sunny clearings. Thus, natural herb mats may be found in patchy clearings within forests up to 13 m tall. They are common in the abandoned *Cocos* plantations of South Island, where *Boerhavia* tends to proliferate into thick mats that completely cover the substrate, vying with *Phymatosorus* and *Ipomoea* for "lebensraum" (Pl. 34). A thick, exposed mat of succulent herbs is found on Noddy Rock, where *Portulaca* is the primary component.

Herb mats occurred on almost every transect, windward and leeward, ranging from 1% to 60% coverage (Figs. 19,23). The most extensive areas (coverage 35–50%) were on Skull, Tridacna, South (Trs. 1,4,6), Emerald, and Mannikiba. Mats predominated in sparsely vegetated areas. Their widths varied according to the age, shape, exposure, and geographic position of the motu but were widest on seaward-facing shores (Table 7).

Wide bands of herb mats may encircle an entire motu; to windward they average 36 m (Table 7), while, bordering the relatively placid and intermittently shaded lagoon, they shrink to a mere 0.9 m. On leeward motus, the corresponding figures are 18.5 m and 4.2 m.

Although reef flats are typically wider wherever an islet turns sharply, it is not unexpected that these perimeter bands are the most extensive on the extremely exposed shores of northern Nake (Pl. 17) and southern South Island. On the latter, they are up to 59 m wide. Similarly, on small exposed motus (e.g., Skull, Noddy Rock), they carpet most of the area (Fig. 27). Under such conditions, *Portulaca* and *Boerhavia* develop much redder stems, possibly due to the presence of a chemical “sunscreen.”

Associations with Birds: Whether bordering the edges of established islands or composing the entire ground cover of tiny motus and ancient reef channels, herb mats are nesting sites for red-tailed tropicbirds, masked and brown boobies, sooty terns, and brown noddies. Herb mats are often used as foraging grounds for shorebirds.

Beach Scrub with Suriana (1.49 ha) (Fig. 20; Pls. 6,24,39,44)

Uncommon on Caroline, beach scrub with *Suriana* is typically found on sand or sandy rubble bordering *Tournefortia* or *Cocos*. On Caroline, it is evidently limited by the paucity of low-lying sand and gravel sheets, with which it is normally associated elsewhere (Fosberg, 1953; Wiens, 1962; Stoddart & Gibbs, 1975).

The following species are present (see Table 2 for abundance indices):

Shrubs: *Tournefortia argentea*, *Suriana maritima*; and

Herbs: *Heliotropium anomalum*, *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Phymatosorus scolopendria*, and *Lepturus repens*.

This plant community was found on 10 motus (Fig. 20), either in thick bands or as scattered shrubs. *Suriana* is most robust on sandy substrates, especially fringing the lower lagoon on South Island (Fig. 36; Pls. 6,24,39) and on windward Tridacna. The fringe, repeatedly interrupted by other species, grows to 12 m wide and 1.8 m high. Here the shrubs are closely appressed and slightly entangled, forming dense shade, which supports a sparse understory. On South, where its roots are submerged at high tide, it is being shaded out by overhanging *Cocos* (compare Pls. 39 and 40), having retreated since 1965. *Suriana* also occurs as scattered individuals or in open bands in coarse rubble. Beach strand up to 60 m wide, containing herb mats, *Tournefortia*, and scattered *Suriana*, were found on South (Tr. 1, Pl. 21), Long (Tr. C), Brothers, Matawa, Long, and the Southern Leeward Islets.

Pandanus Forest (3.38 ha [this figure is pure *Pandanus* forest. Mixed forests containing *Pandanus* account for a further 14.96 ha]) (Fig. 11; Pls. 18,35–38)

Although several species of *Pandanus* are native to the Line Islands, and their seeds are common components of Pacific sea-drift (Ridley, 1930; Stone, 1968), it is probable that the groves of *P. tectorius* on Caroline represent both naturally established forests and cultivars transported by early Polynesians. Its largest acreages are on two islands that contained historical settlements (Nake, South). However, its presence within the interior forests of a few motus lead us to conclude that it may have experienced a dual introduction. On Emerald Isle, 3.20 ha (38% of the islet) supports a mixed forest

of *Tournefortia*, *Pisonia*, and *Pandanus*. Similarly, Shark Islet’s interior woodlands of *Tournefortia*, *Pisonia*, and *Cordia* (5.52 ha, 70% of the islet’s area) also contain a substantial amount of *Pandanus*. The only record of habitation for these motus was a possible hut on Shark. The occurrence of *Pandanus* groves or lone trees on other islets (Fig. 11) is easily attributable to drift seedlings. Dried *Pandanus* seedpods are the most conspicuous litter along Caroline’s lagoon beaches (Pl. 38); its seeds last for months in seawater (Guppy, 1906) and are probably distributed locally by rats and land crabs, as noted elsewhere (Ridley, 1930). Carpels from Nake’s southern mixed woodlands undoubtedly established the grove on *Pandanus* Islet.

The mixed forest with *Pandanus* on south Nake (with *Cocos*, *Cordia*, *Pisonia*, and *Tournefortia*) contains up to 50% *Pandanus* attaining heights of 12 m (Fig. 37). It does, however, look disturbed.

Many *Pandanus* trees were felled on South Island during the coconut planting era (ca. 1873–1925), as we know that they were “somewhat numerous” in 1834 (Bennett, 1840), but only “one or more of the screw pines were found growing in various parts of the island” in 1883 (Trelease, 1884). A drawing in this latter paper (Pl. 50) depicts a grove from South Island denser than any remaining today, where *Pandanus* is uncommon in the beach scrub bordering the *Cocos* plantation.

Trees were fruiting abundantly in September 1988, especially on Nake. The green phalanges, 17.5–20 cm in diameter, ripen to yellow and orange when they fall to the ground. They are eaten by hermit crabs (*Coenobita perlatus* [Pl. 38]).

Tournefortia Scrub and Forest (125.25 ha) (Figs. 24,34; Pls. 5,8,20,30,47,51)

General Distribution: Characteristic of many Pacific islands, *Tournefortia*, a broadleaved evergreen, dominates the wooded motus of Caroline, forming 40% of its total vegetative cover (Fig. 24). Its pale foliage and hemispherical canopies (to 14 m tall) typically surround the taller, darker canopies of *Pisonia* and *Cordia*.

A hardy halophyte, *Tournefortia* occurs on every motu and in every habitat except pure *Pisonia* forest. It is tallest, widest, and lushest on the windward motus, particularly on those where *Pisonia* is also best developed. Without direct sun though, as under dense *Pisonia* or *Cocos*, it withers (Pl. 24).

On other atolls *Tournefortia* forms a narrow or interrupted belt inland of the beach or is a component of mixed scrub (Fosberg, 1953). However, given the floristic poverty on Caroline, especially of shrubs and trees, *Tournefortia* not only has expanded into niches that might elsewhere be occupied by combinations of *Scaevola*, *Pemphis*, *Suriana*, *Terminalia*, *Hernandia*, *Thespesia*, *Hibiscus*, et cetera, but frequently occurs in pure stands (113.03 ha) that extend well inland. It thus occupies a much higher percentage of the islet areas on Caroline than on atolls with greater biodiversity. For example, Nake, the largest islet, has the greatest amount of *Tournefortia* (79.68 ha) of any islet: 28.9 ha of pure scrub and forest, 18.28 ha of “savannah,” 17.48 ha with *Cordia*, 8.99 ha with *Pisonia*, and 6.03 ha mixed with *Cocos*, *Pandanus*, and *Pisonia*.

Overall, we classify *Tournefortia* as a shrub (Stoddart & Gibbs, 1975). However, following Mueller-Dombois *et al.* (1981, p. 58), we also distinguish between its shrub (scrub) and tree communities. Because they intergrade, sometimes we lump them together (vegetation maps and schematic profiles of the motus) and at other times treat them separately (Tables 2,5,10 and ecological discussions):

1. *Tournefortia* Scrub: ≤ 5 m high ($\bar{x} = 2$ m), $<60\%$ canopy coverage (Pls. 20,30,33,47). This open scrub growth is typically confined to islet perimeters or emergent reef channels and covers much of the vegetated rubble on smaller islets. Its species composition is similar to that of the taller forest, except that herbs are more prominent.

2. *Tournefortia* Forest: >5 m high ($\bar{x} = 8$ m), $>60\%$ canopy coverage (Pl. 48). This taller, closed forest, with maximum height 15 m, develops as a second belt of woody vegetation approaching the interior of the larger islets. Figure 34 depicts a schematic profile through pure *Tournefortia* scrub and forest, while Fig. 35 diagrams a profile of a larger islet where *Tournefortia* is represented only on its periphery.

Species Diversity in *Tournefortia* Woodlands: The following species occur in both scrub and forest. Those marked “*” occur primarily in the scrubland (Table 2).

Trees: *Pisonia grandis*, *Morinda citrifolia*, *Pandanus tectorius*, *Cocos nucifera*, *Cordia subcordata*;

Shrubs: *Suriana maritima*, *Tournefortia argentea*, *Scaevola sericea*, Species A;

Herbs: **Heliotropium anomalum*, **Boerhavia repens*, **Portulaca lutea*, **Lepturus repens*, **Laportea ruderalis*, **Achyranthes canescens*, *Phymatosorus scolopendria*, *Ipomoea macrantha*.

Caroline’s tallest *Tournefortia* stands (12–15 m) occur on Nake. On all other windward motus, the *Tournefortia* canopies vary between 6 and 9 m tall, shorter than expected if their forests were virgin. This has historical significance: we do not know the extent of forest felling (if any) on the Windward Islets (Crescent through Tridacna) during the guano era, but we do know that 4,587 coconut palms were planted during 1919–20, and that “misses” (dead seedlings) were fastidiously replaced over the following 2 years (Young, ca. 1922). Thus, their forests, though weed-free today, comprise secondary growth around 60 years old. It is not surprising that *Achyranthes canescens* and *Lepturus repens*, both weedy (though indigenous), are particularly common inland on some windward motus (Figs. 13,16). *Tournefortia*’s rapid recovery illustrates that ecosystems in the pioneer stage generally recover their original condition rapidly when left alone (Fosberg, 1983).

Stature and Area Coverage: Forming an umbrellalike canopy, a typical *Tournefortia* forest is very simple. Its twisted branches and gnarled trunks stretch about untidily over an open understory. The lower branches die off as the trees increase in stature. Sometimes a scant cover of herbs develops in restricted pockets of better soil, such as a clearing where a dead tree fell, a semishaded spot beneath a colony of seabirds, or a site where a storm deposited a few dead fish.

Tournefortia is abundant throughout the atoll. Areas with 90–100% canopy cover were found on Nake (Tr. 4), Long (Trs. B,C,4,6,10,12), North Pig, Pig, North Brothers, Brothers,

Crescent, Arundel (Fig. 34), Tridacna (Trs. 1,2), South (Trs. 1,4), all 5 Southern Leeward Islets, all Central Leewards over 0.5 ha, and Pandanus Islet. *Tournefortia* is present across the entire width of some small motus—for example, Fishball (144 m wide). Even on larger motus such as Mannikiba (280 m wide), *Tournefortia* blankets nearly all the land (Pl. 70). Long (75.98 ha) is a composite motu: long, narrow, and derived from the coalescence of at least five former islets. Because *Tournefortia* encircled the perimeters of these ancient islets, it is now present in five sets of concentric circles, connected by herb mats, down the length of the island (Fig. 39).

In the herb mats, *Tournefortia* is small ($\bar{x} = 1.4$ m) and widely scattered (Table 10). It may be of typical hemispherical shape or irregularly windshorn (Pls. 13,45). On windward coasts they typically form a tight wind barrier one or two trees thick. Moving inshore from the seaward fringe, the trees become progressively taller ($\bar{x} = 6$ m) with a more open understory. *Cordia* often mixes with *Tournefortia*, either as scattered individuals in the understory or canopy, or as small groves. On the Southern Leeward Islets, such belts border the seaward scrublands.

Though still widespread in the Pacific, *Tournefortia* is far less abundant than formerly. On inhabited islands it exists primarily in relict patches or as edging around anthropogenic forests. It rarely covers most of the land area of islets; two exceptions are Taongi (Marshall Islands) and Gaferut (Caroline Islands), both in Micronesia (Fosberg, 1956; Wiens, 1962). The finest quality *Tournefortia* forests on Caroline Atoll (15 m, 80% cover) occupy central and northern Nake (Fig. 37); given Caroline’s history of occupation, these could well be virgin. These 15-m *Tournefortia* compare favorably with 18-m specimens found at Jemo Island by Fosberg (1956). Perhaps Jemo’s trees are at the upper size limit for the species, as *Tournefortia* is generally recorded as 3 to 6 m tall (Wiens, 1962).

Ecology: *Tournefortia* is an integral part of the atoll’s evolution and ecology. Bearing seeds capable of floating for at least 4 months in the sea (Guppy, 1906), it is the first woody plant to establish on tiny motus (<0.1 ha), appearing immediately after the native herbs have begun to germinate in the coarse coral rubble. Requiring little or no soil and adequate rainfall, it can grow up to 2 m a year (Fosberg, 1959). *Tournefortia*’s leaves contribute to soil development, paving the way for plant succession from Stages I through IV, for it only persists in soils that are conducive to the growth of its mesophytic competitors (Fosberg, 1953). The most mature trees ($\bar{x} = 9.5$ m) occur at the *Tournefortia*–*Pisonia* interface, but die off as *Pisonia* expands. When *Tournefortia* has reached its maximum height, most of its lower branches have fallen, leafage is reduced, and flowers and fruits are few. *Tournefortia* usually drops out after one generation. Seedlings are rarely seen in heavy shade, and fallen trees are fairly common on the edge of the interior forests where *Pisonia* replaces it.

An example of complete replacement of *Tournefortia* by *Pisonia* is illustrated by nearby Vostok. It has heretofore been assumed that Vostok’s sole tree species was *Pisonia grandis* (Fosberg, 1936; Bryan, 1942; Clapp & Sibley, 1971b; Garnett, 1983). However, Young (ca. 1922) stated that when Captain J.

Larsen, of the schooner *Papeete*, planted 100 coconuts there on 31 May 1922, he found “*Pukatea* and *Tauhinu* trees, et cetera 60 to 80 feet high;” that is, *Pisonia grandis* and *Tournefortia argentea*, but no “*Tou*” trees (*Cordia subcordata*). By 1935 only *Pisonia* remained (Fosberg, 1936); thus, the last natural *Tournefortia* must have been eliminated by *Pisonia*.

Along some coasts (Long, Nake, South), *Tournefortia* overhangs the water, its roots immersed at high tide. We found floating debris up to 20 m inland within dense *Tournefortia* forest, indicating that this hardy shrub can withstand periodic storms and high tides. If a rosette of *Tournefortia* leaves is placed in fresh water, it droops within an hour, indicating that its tissues require a high salt concentration in order to maintain turgidity (personal observation). Perhaps decreased salinity in the ground water, coupled with reduced light intensity in advanced seral stages, contribute to the eventual disappearance of *Tournefortia* in the center of coral islands.

Associations with Birds: *Tournefortia* is a favored roosting and breeding site for most of Caroline’s seabirds. The taller the trees, the greater the bird diversity they harbor: scrub contained four species (36%) and forest, nine (82%). Sooty terns nest in tight colonies in its shade, its canopies support large populations of red-footed boobies (Pl. 51) and great frigatebirds (Subchapter 1.2, this volume), and its branches are favored by white terns (Figs. 34–36). *Tournefortia* leaves provide nesting material for noddies.

Cordia Forest (1.39 ha) (Fig. 22; Pl. 27)

General Distribution: *Cordia* does not form “the main native woodland” on Caroline Atoll, as implied by Clapp & Sibley (1971a) and stated by Stoddart & Gibbs (1975, p. 104). It occupies far less area than *Tournefortia* or *Pisonia* (Table 9). *Cordia* is generally mixed with other emergents: monotypic *Cordia* forest covers only 1.39 ha, while *Tournefortia* or *Pisonia* containing substantial amounts of *Cordia* total 25.89 ha. *Intoto*, this is less than 10% of Caroline’s woodlands, and *Cordia* is usually subdominant. We treat *Cordia* forest as a separate plant community because of its increasing rarity on Pacific atolls, which makes Caroline’s groves an increasingly important resource in need of conservation. *Cordia* forest occurs primarily on Nake, Windward, Crescent, North Pig, Pig, Danger, Shark, and the Southern Leeward Islets.

History: Bennett (1840) recorded “two species of *Tournefortia*” on Caroline, possibly referring to *Tournefortia* and *Cordia*. There are no other 19th-century records. From *Cordia*’s present distribution we can infer that it was formerly more extensive on South and Nake. Scattered trees within and bordering the *Cocos* plantations suggest that its history is similar to the species on Flint: both Flint and Caroline were worked simultaneously by the same companies for guano (1872–1890) and copra (into the 1930’s). *Pisonia* and *Cordia* forests were felled to make room for coconuts. Several hundred *Cordia* logs were exported from Flint to San Francisco to be used for furniture. The last logs were exported in 1896, 6 years after the guano supplies were depleted, but coconuts were still being planted (Young, ca. 1922). Today, the belt of indigenous vegetation bordering Flint’s coconut plantation still has many large *Cordia* trees (Kepler, 1990b), unlike

Caroline, where today *Cordia* is rare on South Island. However, some of Flint’s *Cordia* trees today may well be those “few tiny, struggling...trees...recently planted” (St. John & Fosberg, 1937).

Abundance and Distribution: *Cordia* seeds are dispersed by ocean currents and can germinate after 40 days in seawater (Guppy, 1906). Requiring the presence of other species (Fosberg, 1953), on Caroline it develops both as an understory shrub and forest emergent (to 15 m high). It typically occupies the woodland periphery, occurring in small circular or linear groves, or mixing with *Tournefortia* and/or *Pisonia* (Table 5). On many other Pacific atolls *Cordia* forms a mixed scrub with *Scaevola* (Fosberg, 1949). *Cordia* may form tall, straight-trunked trees (Pl. 27) or sprawl like *Hibiscus tiliaceus*. In dry rubble sites it may become chlorotic (Pl. 79) or semideciduous. The tallest groves are on Pig (Pl. 27), where six trees averaged 12.6 m tall, 116 cm circumference at 1.5 m high, and 99.8 cm around the trunk base. Lush *Cordia* groves sheltered parts of the upper lagoon on Long Island (Tr. 10).

Flowering times are unpredictable: In November 1989, flowers were abundant, extending through March, yet in November 1990 not one flower was observed (Anne Falconer and AKK, personal observation). Two flowers were seen in September 1988 (personal observation).

Associations with Birds: Black and brown noddies, frigatebirds, and white terns nest in *Cordia* wherever it is a forest component. Great frigatebirds and red-footed boobies favor roosting in the lush, lagoonside forest of *Cordia* and *Pisonia* near the south end of Long Island.

Pisonia Forest (62.17 ha) (Figs. 18,32,33,35,39,41; Pls. 43,52,53; Tables 11–14)

General Distribution: Although *Pisonia grandis* is recorded as “present” in the two previous scientific accounts of Caroline (Trelease, 1884; Clapp & Sibley, 1971a), the quality and extent of its forests has not been recognized. Some stands on this atoll are outstanding representatives of a major ecosystem that was formerly far more widespread in the Pacific.

Common throughout the atoll, *Pisonia* occurs on 29 motus. Well developed groves, 10–21 m tall and up to 359 cm circumference at 1.5 m, are present on 23 of these (Table 11). Although present on motus less than one hectare in size (Table 5), it typically occupies interior forests (schematic profile, Fig. 35), with individual trees or groves contributing from 5% to 100% of the canopy. In general, Caroline’s windward motus support the lushest forests: the maximum height of windward *Pisonia* forests is 21 m; of leeward forests, 15 m.

Mature *Pisonia* forests are monocultures of grandeur. The trees bear one to several stout boles of irregular shape, whose rotting cavities often harbor large coconut crabs or miniponds alive with mosquito larvae. Their scraggly branches occasionally bend over and reroot. It is dark and humid after the glare of the beach. Walking is easy because the forest floor is open except for exposed roots and a scattering of broken branches. Few seedlings occur. Overhead, a constant cacophony of bird calls overwhelms the sound of the trade winds, and guano spills everywhere. Polynesian rats scurry underfoot. It is a curious habitat for a tropical island.

In September 1988 we saw no flowers or fruit. Anne Falconer reported flowers on Motu Ana-Ana in August 1990. *Pisonia* was beginning to bloom on Vostok in March 1990 (A. Kepler, in prep.).

A Historical Perspective: Some of Caroline's most mature *Pisonia* groves (to 21 m tall, 660 cm circumference at 1.5 m, multiple trunks) appear to be virgin. Overall dimensions of the trees, low species diversity, and general character of the plant community are similar to the known virgin groves on Vostok (personal observation, Table 12). We do not have dimensional data (other than height) of these particular areas on Nake, but their level of maturity can be seen in Pl. 43.

Despite the advanced stage of ecological succession of many groves, especially to windward, planting records from 1916–1922 indicate that *Cocos* was planted throughout, not only South, but also on Nake, Long, and all the major Windward Islets (Young, ca. 1922). Given the standard planting density of one tree every 8.5 m² (28 × 28 ft) (Young, ca. 1922), we have calculated the approximate area on each islet given over to *Cocos* plantations, based on the number of coconuts planted (Table 13) times the area required for each tree (73 m²). We have then compared this to the usable areas based on today's forest cover. On all nine Windward Islets, *Cocos* covered 79 to 100% of usable ground; in several cases the amount calculated for *Cocos* exceeds the amount of potentially usable ground. Thus, *Cocos* was so intensively cultivated on the Windward Islets that essentially all the *Pisonia* and most *Tournefortia* forests must have been felled.

Two remarkable points emerge from Table 13: 1. Scarcely any *Cocos* remains today on the nine Windward Islets; seven of them bear no trace of the former plantations (Figs. 43,44,47,48); and 2. recovery of Caroline's natural ecosystems, Stages I through V (Ecological Succession section), on the windward side has been rapid and, at least on Brothers Islet (Fig. 46), reasonably complete with regard to ecological succession and species diversity. Today the Windward Islets have the lushest and tallest plant communities, with higher species diversity than the leeward islets (Table 3), which have evidently experienced far less human disturbance.

This differential disturbance on the windward and leeward sides of the atoll explains enigmas such as 20-m-tall *Pisonia* forest on the leeward Booby Islet (0.84 ha), taller than most of the windward forests; the absence of *Pisonia* on windward Tridaena Islet (9.08 ha), which, being close to South Island, probably supported *Cocos*, which was managed longer than the more distant windward islets; and the patchy distribution of *Pisonia* in the interior of several islets (e.g., Windward, Arundel). This last point also applies to Mannikiba (21.49 ha), the largest leeward islet. According to Young (ca. 1922), 6,000 seed sets were brought from Flint to Caroline in 1920 and kept on Mannikiba. This "nursery stock" was used to replant "misses" on other islets, due mostly to destruction by coconut crabs and poor planting. Today, Mannikiba's total acreage of *Pisonia* (Fig. 53) is very small and fragmented relative to the islet's size: 1.13 ha, 5% of the total land area. Compare this with Bird Islet (Fig. 55), which, as far as we know, has never been disturbed: 1.70 ha *Pisonia*, 42% of the islet's land area.

On both Caroline and Flint there is much variation in the quality of the regenerated *Pisonia* forests (Table 12). Some trees bear enormous, partly rotting holes, black algae smothering the bark, multiple trunks, and few or no understory herbs. Other trees are tall and straight-trunked, with characteristic whitish bark, and bear no rotting holes in their bases. Such observations suggest that when their indigenous forests were felled, only minimal cutting was done, and many *Pisonias* were able to regenerate quickly by sprouting from rooted stumps and fallen branches. This speculation is supported by the fact that some of Vostok's *Pisonia* trees regenerated similarly. Maude (1953, p. 96) stated that "there is room for 8,000 palms on Vostok, but only 100 have been planted and most of these have been choked in the luxuriant 'buka' (*Pisonia grandis*) forest: no attempt having been made to exploit the island since the initial planting."

Pisonia, a soft, pulpy wood, has a well-known ability to sprout or send up suckers from dismembered branches or fallen trunks (Fosberg, 1953), and it has been noted that older trees are virtually indestructible, fire being the only effective means of clearing forests (Wiens, 1962, p. 397). The senior author has photographed leaf sprouts from partly burned twigs as small as 1 m long and 5 to 6 cm in diameter.

Since the existing *Cocos* plantations on South Island and southwest Nake contain few *Pisonias*, it seems that forest clearing was more thorough on the atoll's larger islets than on the smaller ones, which today manifest scant traces of their former history. Fortunately for Caroline, its coconut plantations were plagued by a number of problems, which resulted in their being abandoned twice: coconut crabs, seabirds, rats, *Ipomoea* vines, and an unknown disease (see under Coconut Woodlands, this section).

A footnote in Young (ca. 1922, p. 15) stated that "the larger portion of the 30,000 trees planted were either badly planted or smitten with some disease as in 1927 it was reported by Mr. Bunckley that most of them had perished." In 1929 only 13,215 trees were left and more were being planted. Considering the distribution of both palms and natural forests today, it appears that plantations continued on South and Nake and were abandoned on the smaller islets, allowing for a better recovery than might be expected had the *Cocos* grown to maturity.

Once a *Cocos* plantation has been well established and subsequently abandoned, *Pisonia* regrowth is more difficult. This is characteristic of many islands in the tropics. For example, on Cousin Island (an ICBP wildlife preserve since 1968, Seychelles Islands, Indian Ocean), where *Pisonia* is currently reestablishing within a deteriorating *Cocos* plantation, Phillips & Phillips (1990, p. 37) envisioned "centuries rather than decades before something like a natural ecosystem develops." We predict a similar time frame for areas on Caroline and Flint where *Cocos* canopy is over 70% cover.

Annual Growth Rates: Data on *Pisonia grandis* growth rates are evidently lacking. On Cousin Island, vegetation changes, including *Pisonia* and *Cocos*, have been monitored since 1974 (Phillips, 1984; Phillips & Phillips, 1990). However, as no measurements of any tree dimensions are included, growth rates cannot be deduced.

Because of this paucity of data on *Pisonia*, and because its forests have diminished significantly on coral islands this century, we are presenting our data from Caroline, with comparisons with Vostok and Flint, in the hopes that it might inspire more research.

One point is clear: on all three of the Southern Line Islands, *Pisonia grandis* has recovered fast from disturbance (except for total forest elimination), reaching close to its maximum height and ecological maturity in 70 years or less. Mature *Pisonia*, under optimal conditions of soil, temperature, and rainfall, may attain 35 m, as on Fanning and Washington (Garnett, 1983 and personal communication). However, in the Southern Line Islands, canopies of similarly virgin *Pisonia* on Vostok rarely exceed 25–30 m tall (Kepler, 1990c).

Caroline's prime grove—21 m tall, with circumferences (at 1.5 m) to 660 cm, and bearing multiple trunks and root suckers—we now know date back only to the 1920's. They have thus averaged a growth rate of 0.32 m per year since, say, 1925 (65 years). Growth was undoubtedly fastest during the first few years.

Further evidence of fast growth rates is provided from Flint Island. In 1934 only one small *Pisonia* was recorded (St. John & Fosberg, 1937). Fosberg (personal communication) recalled that only scant traces of native vegetation existed at the time, virtually the entire island (324 ha) being planted with *Cocos*. In 1990, transect surveys (Kepler, 1990b,d), coupled with an analysis of aerial photographs, revealed that single to multi-trunked *Pisonia* trees, now quite common on the windward side of Flint, attained maximum heights of 30 m, having circumferences at the base and at 1.5 m of 1,000 cm and 200 cm, respectively (Table 12). These compare favorably with one large *Pisonia*, presumably virgin, measured on Atafu Island (Tokelau) by the US Exploring Expedition in 1840, which was more than 600 cm in circumference at its base and about 12 m tall (Wilkes, 1845, Vol. V, p. 9). Furthermore, indigenous forests (*Pisonia*, *Cordia*, *Guetarda*), with canopies of 4 to >20 m, covered 57 ha, 28% of Flint's vegetated area. Thus, numerous *Pisonias* have not only established themselves since the plantation was abandoned in the late 1930's but have averaged approximately 0.5 m growth per year. This faster growth rate than on Caroline may be due to Flint's higher rainfall and greater relative humidity due to the presence of a more successful coconut plantation inland: Caroline's annual output of copra was 15 tons, compared to 230 tons for Flint (Young, ca. 1922; Maude, 1953).

Species Diversity in *Pisonia* Forests: Caroline's motus harbor every stage in the development of a *Pisonia* forest, from stately monotypic groves to a single tree. The plant communities between these extremes harbor the greatest species diversity and most luxuriant growth on the atoll. The following species are present (Table 2):

Trees: *Morinda citrifolia*, *Cordia subcordata*, *Cocos nucifera*, *Pandanus tectorius*, *Pisonia grandis*;

Shrubs: *Tournefortia argentea*; and

Herbs: *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Lepturus repens*, *Achyranthes canescens*, *Phymatosorus scolopendria*, and *Ipomoea macrantha*.

The number of species within *Pisonia* forests ranges from 1 to 14 (Table 14). As *Pisonia* becomes more dominant, their trees are taller (21 m), and species diversity is less (Table 14). Here, the average number of species is 3.4. Species diversity is also very low at the other extreme of *Pisonia* development: in one young motu (Azure), only a single 6-m-tall *Pisonia* tree is present (\bar{x} = 4.0 m). The smallest islet on which we found *Pisonia*, Azure is only 0.20 ha in area and 77 m wide (Fig. 55, Pl. 53); more than half of it is rubble. The width of its scrub is only 38 m. Along a transect within the majestic *Pisonia* grove (100% canopy cover) on Brothers (Fig. 46), we found no other plant species, an extreme case of the barrenness of *Pisonia* understory. This grove, 13 m tall and extending 42 m from east to west, was sharply delineated from the 6-m-high *Tournefortia* forests on both sides and provides a striking example of complete ecological succession since its *Cocos* plantation days of the 1920's.

The highest species diversity occurred with mixed co-dominants (*Tournefortia*, *Cordia*), and *Pisonia* coverage 25–50% (Table 14). Here, the average number of species was 6.2 (range 3–10). Regardless of the area or width of the motu on which they occurred, these mixed stands (\bar{x} = 7 m tall) were always shorter than pure *Pisonia* forest.

Ecology: On Caroline, most plant species are established early in the evolution of individual motus, increasing in abundance and stature while the motus are quite small. *Pisonia* typifies this pattern: single trees occur on 2 motus whose areas are only 0.2 ha (Table 6). This suggests that *Pisonia* is partly salt-tolerant, at least in its early growth stages. In general, however, motus less than 0.7 ha on Caroline have little *Pisonia* (Table 6). It is difficult to imagine a freshwater lens on Motu Nautonga (1 ha), where an 11-m-tall *Pisonia* forest is found (Table 11). Further evidence for the salt-tolerant nature of *Pisonia* comes from Vostok, where a *Pisonia* forest, the sole woodland, extends to the edge of the shoreline rubble and herb mat. The trees, tightly pruned by wind and salt, have no buffer of coastal scrub. During storms, seawater reaches Vostok's interior forest, yet this 24-ha island supports one of the largest and tallest (25 m high) groves in the Pacific (Clapp & Sibley, 1971b; Fosberg, 1977b and personal observation).

Many *Pisonia* trees were heavily infested with scale insects (Coccidae) and Neuropteran larvae (*Chrysopa* sp.), identified by Dr. Scott Miller (Bishop Museum, Honolulu, Hawaii). This appears to be a natural phenomenon, as they were also abundant on the virgin *Pisonia* forests on Vostok and also on secondary *Pisonias* at Flint.

Relationships Between *Pisonia* Forest Height and Motu Dimensions: Contrary to expectations, the tallest, most mature forests did not all occur on the largest motus (Table 11). The three prime forests (90–100% canopy cover) are on Nike (107.46 ha), Pig (7.21 ha), and Booby (0.84 ha). Trees on Booby are smaller in girth than those on Nike and Pig, but their height (20 m) is impressive; as far as we know, Booby was never cleared. Fine forests occur on other small, undisturbed motus; for example, *Pisonia* grew to 14 m on Raurau (3.48 ha) and to 11 m on Kimoa (1.80 ha).

A positive correlation exists between *Pisonia* height and island width (Fig. 32). On Caroline, motus were 90 m wide before closed canopies of 13 m developed (Fig. 32), and tree height increased to 21 m with islet width up to 200 m (Fig. topmost star in Fig. 32). Further increases in islet width did not result in taller trees. However, even on motus with sufficient width, *Pisonia* did not develop unless other environmental conditions were suitable. For example, on Long, *Pisonia* only occurred in the centers of its former islets, not in the scrubby areas where coalescence is more recent. *Tridacna*, seemingly excellent for *Pisonia*, has not yet recovered from its *Cocos* plantations.

***Pisonia*–Seabird Relationships:** Seabirds are an integral part of *Pisonia* ecology. Its sticky seed capsules adhere to the feathers of, and are thus dispersed by, seabirds such as terns, boobies, and frigatebirds; thus, its early appearance on small motus is not surprising.

On Caroline, six species of seabirds nest in its branches, dropping considerable guano to the ground below. Black noddies, amassing in dense colonies, nest almost exclusively in *Pisonia*, along with brown noddies, white terns, great and lesser frigatebirds, and red-footed boobies. Pig Islet, with 7.25 ha of excellent *Pisonia* forest, supported a dense colony of nearly 2,000 pairs of black noddies (Subchapter 1.2, this volume). Bristle-thighed curlews feed on the ground beneath its open understory, and the long-tailed cuckoo forages within its canopy.

Seabirds may be so much a part of *Pisonia* ecology that a debate exists as to whether *Pisonia* actually requires guano for successful germination and establishment of seedlings (Shaw, 1952; Fosberg, 1953; Wiens, 1962). Very high phosphate and nitrogen levels are associated with mature *Pisonia*, and concurrently the development of *Pisonia* forest results in greatly modified soils that perpetuate its existence (Wiens, 1962; Spicer & Newbery, 1979). The formation of a highly acid raw humus on the surface of the ground, sometimes in association with phosphatic hardpan, has also been documented on several atolls by Fosberg (1953, 1956), including Vostok (AKK and John Phillips, personal observation). Perhaps *Pisonia*'s present distribution, primarily restricted to uninhabited islands (Shaw, 1952; Wiens, 1962), is in part due to the fact that its primary seed carriers, seabirds, rarely coexist for long with man.

Remnant *Pisonia* Forests in the Pacific: Though naturally and widely distributed from the western Indian Ocean to the eastern Pacific (excluding Hawaii), *Pisonia grandis* has become increasingly rare this century (Fosberg, 1953 and personal communication). Occupying the interior of most atolls, it may have formerly covered the greatest area of any tree species in the Pacific (Wiens, 1962). Shaw (1952), summarizing its distribution, stated that it only occurs on remote, generally uninhabited islands ranging from the western Indian Ocean to the eastern Pacific, including Malaysia. However, more recent studies, particularly by Fosberg, indicate that because its habitat occupies, and is in part responsible for, the most fertile areas of inhabited islands, its formerly extensive forests have been largely replaced by coconuts. Though *Pisonia*'s soft wood is

of little use to either atoll inhabitants or to the timber industry, its soils were rich sources of phosphate fertilizer and were thus greatly disturbed during the guano mining era.

One of the most extensive *Pisonia* stands in the Pacific (13.5 ha on Vostok) was partly burned in 1977 by members of a "scientific expedition" (Fosberg, 1977b). The Royal New Zealand Air Force found it smoldering 3 months later (Fosberg, 1977b, personal communication). In a March 1990 visit to Vostok, we found that approximately 1.5 ha were completely cleared (Kepler, 1990c), and a further unknown amount of land was affected. Other excellent groves exist on Palmyra and Washington (northern Line Group) and on Nikumaroro (Phoenix Group). Flint (Southern Line Group); Christmas (northern Line Group); Bikar, Jemo, and Ujae (Marshall Islands); and Aitutaki, Penrhyn, Suvarrow, and Manihiki (Cook Islands) have relatively small stands. Caroline, with 62.73 ha in *Pisonia* forest (36.94 ha in monotypic groves) holds some of the finest representatives of this ecosystem in the Pacific, even though much of it is not virgin.

Coconut Woodlands (96.14 ha) (Figs. 14,36; Pls. 18,23,24, 28–30,33,34,37,39,40,44)

General Distribution: *Cocos*, although present on 15 motus and known historically from another 4, covers significant areas only on Caroline's 2 largest islets, South and Nake (Table 13). Individual trees and small groves elsewhere are drift-derived or remnants of plantings made from 1916–1920.

The following species occur in habitats containing *Cocos* (Table 2):

Trees: *Pisonia grandis*, *Morinda citrifolia*, *Pandanus tectorius*, *Cordia subcordata*, *Cocos nucifera*, *Thespesia populnea*, *Hibiscus tiliaceus*;

Shrubs: *Tournefortia argentea*, *Ximenia americana*; and

Herbs: *Boerhavia repens*, *Portulaca lutea*, *Laportea ruderalis*, *Achyranthes canescens*, *Phymatosorus scolopendria*, *Ipomoea macrantha*, *Lepturus repens*, *Tacca leontopetaloides*, *Psilotum nudum*, *Phyllanthus amarus*, and *Sida fallax*.

The distribution of *Cocos* (Fig. 14), in order of decreasing abundance is as follows: South: Forests old and neglected. Healthiest palms line the lagoon, currently shading out strip of native scrub. Nake: Southern forests (50–80% *Cocos*) healthier, younger, with more native trees and *Pandanus* than on South; grove of about 50 palms on northeast. Long: Range from <1% cover (Tr. C) to dense fringe adjacent to lagoon. Emerald: Northeast and center-west patches. Mannikiba: Main grove, northeast: 40 palms, 20 m high, another patch in south center. Ana-Ana: House site, northeast point. Bird, Blackfin, Brothers, Nautonga, North Brothers, Pig, *Pisonia*, Raurau, Shark: Few trees each, primarily in *Tournefortia*. Lone Palm: One tree, central forests.

History: A relatively small coconut grove was planted on South Island prior to the 16th century by Tuamotuan settlers (Emory, 1947; Maude, 1968). In 1606, de Quiros noted "plenty of palms" and "many cocoa-nuts" (Markham, 1904). Since then, every visitor has recorded them as they grew, and still grow, adjacent to the boat "landing." A smaller grove evidently also existed in the south-southwest portion of South Island

(Lucett, 1851). According to Maude (ca. 1938), palms were also periodically planted—and destroyed—“by whalers and other chance visitors to the island.”

Until Arundel's arrival in 1885, *Cocos* was basically confined to this single grove in the northwest sector of South Island (Maude, ca. 1942a). In 1885, land clearing began, and from then till 1929, nearly 38,000 palms were planted, 29,480 between 1916 and 1920 and another 7,000 young trees after 1927 to replace thousands that had perished (Young, ca. 1922). Arundel's initial license gave him the exclusive rights to occupy Caroline and Flint, planting coconuts and other trees for 21 years, in return for an annual rental of 50 pounds (Maude, ca. 1942a). In 1929, 13,215 trees remained, after which no one has counted them. Our field work and scrutiny of aerial photographs indicate that far fewer exist today.

Caroline's plantations produced copra periodically from 1873 to 1934, but never profitably. They suffered greatly from the atoll's abandonment from 1901–1916. Dying and poorly planted palms presented continual setbacks (Young, ca. 1922), and in 1878 a hurricane wrought great destruction (N.I.D., 1943). In addition, plantation managers lamented their poor productivity due to choking “by undergrowth and Pohue Vine [said to be *Tuumfetta* (= *Triumfetta*) *procumbens*, most likely a misidentification of *Ipomoea macrantha*], destruction of inflorescences by great numbers of seabirds which roosted in the tops and broke off the flowers as they appeared,” disease, and ruination of nuts by Polynesian rats and coconut crabs. As a result of this, the resident laborers slaughtered many crabs, and “greatly reduced the numbers of sea birds, who migrated to unoccupied islets.” The rat problem was never resolved and appears to be the major reason for repeated failure of the plantations on both Caroline and Flint. Their enormous numbers and voracious eating habits greatly reduced both the crops of potentially healthy nuts as well as the volume of dried copra. In 1920, 4,600 were trapped on South Island, and hundreds more were killed by small terriers introduced specifically to control them (Young, ca. 1922). Maude (personal communication) recalls that one terrier still survived in the 1940's. Rats still abound, especially within coconut groves and *Pisonia* forests. Another serious problem was due to coconut crabs digging up recently planted nuts and also their habit of pinching off young developing shoots. Evidently after the palms had attained one year's growth this was no longer a problem (Young, ca. 1922).

Before abandonment (1902 to 1916, and after 1934), Caroline's plantations were owned by several companies whose average annual copra output was approximately 14 tons. From 1934 to the 1970's, copra was harvested sporadically by small parties from Tahiti (Garnett, 1983), but within the last 2 decades it stopped altogether.

Despite the relatively fertile soils of South Island, the problems in the plantations hampered the establishment of permanent settlements on Caroline. In the 1930's, Maude estimated that the atoll could support 400 Gilbertese, increasing to over 1,000 “when the island has been fully planted” (Maude, ca. 1938). However, colonists were never established, leaving Caroline “one of the least spoiled islands in the Pacific”

(Stoddart, 1976). As Young's (ca. 1922) unpublished “Memoranda” indicate, Caroline is not as pristine as it appears; however, the rapid comeback of many of its natural forests on the windward side is remarkable (see discussion under *Pisonia* Forests, this section).

Distribution and Abundance: We recognize four subdivisions of the coconut woodlands: *Cocos* Plantations, Dying *Cocos-Ipomoea* Plantation, Scattered Groves on Small Motus, and Mixed Forest with *Cocos*.

1. *Cocos* Plantations (34.07 ha)

Palm forests now dominate South Island and southwestern Nake. Although the planting of *Cocos* on South altered most of its original habitats, Nake escaped with less damage; whereas *Cocos* covers 77% of the area on South, it takes up only 6% of Nake (11% including mixed forests). The 60 to 100-year-old trees form tall, closed canopy woodlands (Pl. 24) 21–25 m high, the customary maximum height recorded for old plantations (Fosberg, 1953). Figure 51 shows the distribution and abundance of plant species along a transect running centrally through the island, while Fig. 36 depicts a schematic profile of the same swath.

Pure coconut plantations (like all habitats on Caroline) harbor relatively few species: up to 7 trees, zero to 2 shrubs, and 5–11 herbs. The ground vegetation and shrub layers are composed almost exclusively of indigenous species, an unusual feature. However, skirting the edge of South Island's lagoon, tall palms overhang the water and crowd out native plants; there were considerably fewer *Suriana* and *Tournefortia* in 1988 (Pl. 29) than in 1965 (Pl. 40).

2. Dying *Cocos-Ipomoea* Plantation (53.92 ha)

Mature plantations characteristically become overgrown with shrubs and vines (Fosberg, 1953, 1956). *Ipomoea macrantha*, the sole vine on Caroline, forms tangled, impenetrable thickets. Indigenous, nonparasitic, and widely dispersed by ocean currents, it occurs naturally in small numbers in natural habitats on Caroline, but grows rampantly in disturbed areas. These vine-covered coconut woodlands cover two-thirds of South Island's interior (Fig. 50). The Dying *Cocos-Ipomoea* forest is moribund. It is bordered by a belt of living palms, which in turn are sheltered by a narrow rim of indigenous vegetation (Figs. 36, 51).

While surveying the South Island transects, the authors stomped over intertwining thickets up to 3 m high (Pl. 7) and crawled through tightly-knit masses of vines descending from the crowns of old palms, *Pisonia*, and *Morinda* bushes, until this too, proved impenetrable. In sunny clearings dotted with dead or dying palms, *Ipomoea*, *Boerhavia*, and *Phymatosorus* proliferated luxuriantly. *Ipomoea*, one of the prime reasons for the double abandonment of copra production, will continue to destroy the coconuts, encouraging natural ecological succession to begin anew.

3. Scattered Groves on Small Motus (0.82 ha)

Drift-derived palms were observed as long ago as 1834 (Bennett, 1840). In 1916, when planting operations were commenced after a break of 14 years, about 40 trees grew beyond the plantations (Maude, ca. 1942a). Today, small

Cocos groves, up to 50 palms, drift-derived and plantation remnants, generally close to the shoreline (Pls. 29, 30), occur on 11 motus.

4. *Mixed Forest with Cocos* (6.24 ha)

This forest type is a simplified version of more complex and varied mixed forests that occur on most inhabited atolls. Composed of both anthropogenic and native elements, it contains a high proportion of *Cocos* (50–80%) mingled with variable proportions of *Tournefortia*, *Pisonia* and *Pandanus*. This forest type occurs primarily in southern Nake (Fig. 14), but also on Emerald, Shark, and southwest Long, where it mixes with *Cordia* and *Tournefortia*.

House Site: A single clearing on Motu Ana-Ana, approximately 40 m × 70 m, contains a few *Cocos* adjacent to a vegetable garden and thatched living quarters (Pl. 53).

Associations with Seabirds: *Cocos*-dominated habitats were the most depauperate on Caroline: only brown noddies and white terns breed there (Pl. 54). The noddies nest high within the frond and inflorescence bases, whereas the white terns preferred lower sites. The absence of other species suggests that the anthropogenic *Cocos* forests seriously inhibit seabird use and may continue to do so for decades until they are replaced by native vegetation.

Absent Plant Communities

Caroline's impoverished flora and simple geology has resulted in a limited variety of ecosystems. The atoll is thus notable not only for its grand *Pisonia* forests, extensive monotypic stands of *Tournefortia*, and presence of *Cordia* groves, but also for the absence of several ecosystems that are generally considered typical of Pacific atolls:

1. *Sesuvium* flats;
2. *Pemphis*, *Scaevola*, and *Sida* scrub (two *Scaevola* plants are present, and the only two *Sida* records are from 1884 and 1990);
3. *Barringtonia*, *Calophyllum*, *Guetarda*, *Hernandia*, and *Ochrosia* forests;
4. Plant associations (except *Cocos*) typical of native cultures on atolls: breadfruit groves (*Artocarpus altilis*), taro pits (*Cyrtosperma chamissonis*, *Colocasia esculenta*, *Xanthosoma sagittifolia*), cultivated ornamentals (*Hibiscus rosa-sinensis*, *Plumeria* spp., et cetera), or weedy grasslands/wastelands (*Paspalum*, *Sporobolus*, *Wedelia*, *Vigna*, et cetera). Even widespread introduced strand species such as *Terminalia catappa* and *Casuarina equisetifolia* are absent.

In addition, there are no mangroves, peat bogs, marshes, ponds, salt flats, or other habitats associated with fresh or brackish water. Poorly represented are:

1. *Lepturus* grassland. Although *Lepturus* is present in coastal herb mats, and occasionally in patches within the forest understory, it does not form a separate plant community. However, it may once have covered the extensive clearings on South Island (Pl. 2).
2. Mixed forest. Though 6.24 ha of mixed forest (with *Cocos*) occurs (primarily on Nake), it is of such minor importance to Caroline's overall vegetation that it is treated as a subsection of coconut woodlands.

Description and Ecology of the Motus

These islet accounts synthesize the history, physiography, vegetation patterns, ecology, seabird colonies, miscellaneous biota, and the effects of human activity (if any) on Caroline's 39 motus (Fig. 2). Mapping is based on the coast-to-coast transects, perimeter surveys, complete surveys (smaller motus), color transparencies, and aerial photographs.

All motus are detrital reef islets representing many evolutionary stages from barely emerged coral rubble to large islets with relatively fertile "soils" supporting lush vegetation. There is one tiny old reef platform in its final stages of erosion.

We discuss and map them in geographic order beginning in the north with Nake and progressing down the windward reef through Long and the 13 Windward Islets to South Island. Beginning anew in the north, we move south through 7 South Nake Islets, 11 Central Leeward Islets, and finally the 5 Southern Leeward Islets.

Because of the variety of islet shapes, "long" or "length" refers to the longest dimension lying parallel to the outer reef edge (normally north–south) and "wide" or "width" to the longest dimension perpendicular to the outer reef edge (normally east–west). South Island, the only exception, is considered to lie adjacent to the southern reef edge, so its "length" is measured east–west. Seabird numbers are from Subchapter 1.2, Table 1, this volume. For convenience in locating particular islets, the order is as follows:

1. Nake Island (Fig. 37)
2. Long Island (Fig. 38)

Windward Islets

3. Bo'sun Bird (Fig. 42)
4. Windward (Fig. 43)
5. Crescent (Fig. 43)
6. Atibu (Fig. 43)
7. North Pig (Fig. 44)
8. Pig (Fig. 44)
9. Skull (Fig. 44)
10. North Brothers (Fig. 44)
11. Brothers (Fig. 44)
12. Noddy Rock (Fig. 47)
13. North Arundel (Fig. 47)
14. Arundel (Fig. 47)
15. Tridacna (Fig. 48)
16. South Island (Fig. 50)

South Nake Islets

17. Pandanus (Fig. 52)
18. Danger (Fig. 52)
19. Booby (Fig. 52)
20. Coral (Fig. 52)
21. Lone Palm (Fig. 52)
22. Kota (Fig. 52)
23. Mouakena (Fig. 52)

Central Leeward Islets

24. Mannikiba (Fig. 53)
25. Blackfin (Fig. 54)
26. Matawa (Fig. 54)
27. Emerald (Fig. 54)
28. Shark (Fig. 55)
29. Scarlet Crab (Fig. 55)
30. Nautonga (Fig. 55)
31. Azure (Fig. 55)
32. Reef-flat (Fig. 55)
33. Bird (Fig. 55)
34. Fishball (Fig. 55)

Southern Leeward Islets

35. Raurau (Fig. 57)
36. Eitei (Fig. 57)
37. Pisonia (Fig. 57)
38. Kimoa (Fig. 57)
39. Ana-Ana (Fig. 57)

1. NAKE ISLAND (91.72 ha) (Figs. 30,37; Pls. 18,23, 35–37,43)

History: Nake's large size and underground water lens, coupled with topography and soils more varied than elsewhere on Caroline, attracted early Polynesian settlers. Because early European visitors stayed primarily on South Island, there is only a single reference to *Cocos* prior to the late 19th century (one tree seen in 1825 by Paulding [1831]).

The far northwest of Nake (also called North Island in Young, ca. 1922) houses the most important archaeological site on Caroline—a large *marae* (Figs. 3,37; Pl. 36). Discovered during the guano era, the site is marked as “graves” on Arundel's map. Arundel, who was living on the atoll when the *marae* was discovered, describes it thus: “On the north-west end of Caroline are some curious old native remains, whether places of burial or of sacrifice I cannot determine. I opened one of these, but could find no indication whatever to guide me in a decision” (Arundel, 1890). The senior author, R. Falconer, and G. Wragg located, measured, and photographed this *marae* in 1990. The entire courtyard was approximately 18 m long by 14 m wide. All 10 peripheral stones and the central one were easily identifiable from the 1883 plan (Fig. 3), although a few had fallen over or broken due to encroaching vegetation. The lower wall, partly destroyed by Arundel, had not been reconstructed. It is probable that this *marae* had not been seen since the 1880's; though discussed by Emory (1947), he never visited Caroline personally.

Northwest Nake is particularly suitable for a place of worship and sacrifice: it fits most of the environmental criteria indispensable to ancient Tuamotuan religious ritual (Emory, 1947). First, flat ground was necessary, preferably lying at right angles to, or parallel to, the lagoon. Second, it was important to have the wind blowing across the *marae* to waft away the smells of sacrificed animals. Third, ceremonial items included branches of the *Pisonia* tree, leaves of *Cocos* (for leaf

charms/“rosaries”), and the aerial roots of *Pandanus*. Fourth, feathers from “black terns” (black noddy), frigatebirds, and red-tailed tropicbirds were also necessary for rituals. Rather than a smooth substrate, the early Polynesians would have had to be content with leveled coral rubble and distance from the lagoon. The only organism not living near the *marae* today is the tropicbird; however, their elongated tail feathers could have been plucked from adults nesting on nearby motus.

Since *marae* are sacred places, there is possibly a meaning to the location of the main “courtyard” close to the atoll's northern tip. Generally the northern extremities of islands were auspicious places for Polynesians; it is here, they believed, that disembodied spirits were whisked to the netherworld.

Physiography: Largest in area, Nake is the northernmost motu, separated from Long by a 40-m channel (Pl. 18). With maximum dimensions 2,000 m long and 685 m wide, it is basically rectangular with rounded corners and a peninsula-like extension in the southeast.

Nake lies north of the lagoon, having a southern “bay” (which we named Sandy Inlet), in which silt, sand, and fine coral debris are being actively deposited (Pl. 23). Sandy Inlet, a hard, flat expanse of fine lagoon mud and sand, is 145 m wide at its mouth and extends 200 m north into the main islet. Its 3.50 ha provide a favorite feeding location for shorebirds, especially bristle-thighed curlews. If Arundel's chart (Fig. 4) is correct, Sandy Inlet has increased its land area during the last century.

On the reef flats off the west side are extensive remnants of jagged upraised reef (Pl. 11) and occasional beachrock. The exposed beaches and reef flats at Nake's north point are especially broad, characteristic of reef flats at the exposed corners of islands. Comparisons of the northern sweep of rubble on recent aerial photos with Arundel's map indicate that much coral debris, in the form of raised ridges (Pl. 17), has been added since 1883. In the deep, fine coral rubble mixed with sand east of the *marae*, the 1990 expedition found three old turtle nests. Overall, unvegetated coral rubble, mud, and sand account for only 6% of the land area. In addition, some sparsely vegetated expanses of hardpan were noted in the south-central sector, just inland of the coast within a belt of *Tournefortia* forest.

Nake's windward coast, complete with a peaked beach crest and discontinuous beachrock, is 30 m wide in the north, narrowing to 3 m in the south. Offshore, submerged reef flats form a sandy moat bordered by a barrier reef upon which waves pound incessantly.

In the distant past, what we now call Nake consisted of two separate motus. Aerial photos (Chapter Frontispiece) reveal an oblique, ancient channel about two-thirds of the way down the islet. It is now well vegetated in the center but scrubby near the coastlines.

Vegetation: There are 16 plant species (5 trees, 1 shrub, 10 herbs), 59% of Caroline's flora. Nake is the lushest motu. Its woodlands (82.39 ha) are about 80% native and 20% with *Cocos* (Pl. 37). Although in 1916 there were about 260 palms, and the entire island was evidently planted with 10,544 palms in 1918–1919 (Young, ca. 1922, Table 13), substantial tracts of each major vegetation type occur today. Its interior is rich in

Pisonia, with the largest acreage (20.79 ha) and some of the tallest trees (20 m high) on the atoll (Pl. 43, Table 11). In addition, *Cordia* is well represented: two major groves of *Cordia-Tournefortia* forest occupy 11.8 ha, 2% of Nake's area. Extensive pioneer herb mats, flanked on their inner sides by *Tournefortia* scrub, occur in the north and east. The remaining *Cocos*, essentially in the southern quarter, comprise Caroline's second largest coconut grove.

Birds: Nake, with 80% of Caroline's breeding seabird species, shows a direct correlation between islet size and bird species diversity. Nine species of seabirds breed, all with larger populations (pairs) than previously reported (Clapp & Sibley, 1971a): masked booby (105), brown booby (1), red-footed booby (496), great frigatebird (522), lesser frigatebird (56), brown noddie (390), black noddie (814), sooty tern (nesting in 1989; Anne Falconer, personal communication), and white tern (1,094).

2. LONG ISLAND (75.98 ha) (Figs. 30,35,38–41; Pls. 8,13,18,20,28,33,47,58)

Third largest in area, this longest of motus covers nearly one-third of the atoll's windward side. In the north it is separated from Nake by a narrow channel; from its southern tip a chain of smaller motus extends south along the windward reef.

Physiography and History: Long—4,226 m long and 330 m wide—is somewhat snake-shaped, with an enlarged northern "head" and attenuated "tail." From a distance its vegetation appears as a series of humps. Long has experienced a fairly complex geological history, noted by the Solar Eclipse Party: "On some of the islands there are spaces void of vegetation, extending from lagoon to beach, which indicate the existence at a former time of a water separation" (Holden & Qualtrough, 1884).

At present, Long is composed of five distinct former islets separated by sparsely vegetated channels of coarse sand and coral gravel. Aerial photographs also reveal further, older subdivisions (discussed below). Coalescence and fracturing of the original motus have probably occurred repeatedly. Since erosion proceeds faster on an atoll's windward reefs, providing coral fragments, coralline algae, and pulverized mollusks, it is no surprise that the first series of Caroline's motus to fuse were those facing this rich source of parent material.

Long's coarse rubble beaches (Pls. 13,20) are a mirror image of those on Nake: southward, they widen progressively. The swath of unvegetated rubble above high tide line in the upper two-thirds of Long averages 8 m wide, while in the lower third it is 40 m wide. Unvegetated coral debris accounts for 10% of the island's area (Fig. 30). Beachrock, flanking the windward shoreline for most of its length, is more abundant than elsewhere on the atoll (Pl. 58).

Long's lagoon flank is edged with submerged sand and silt and is one of the most sheltered parts of Caroline. Sand and rubble deposition off the south point has formed an islet in the lagoon (Bo'sun Bird), which could, in the future, coalesce with Long's south point to form a hook.

An uncommon substrate on Caroline, upraised reef (*makatea*) forms a low rampart (generally <1 m high) paralleling the ridge crest inside the vegetation for much of the lower quarter of Long.

In 1990 Graham Wragg found some scattered large stones, similar to those of the *marae* on Nake, located centrally 100 m north of the southern tip of Long, confirming the report of the remains of a smaller *marae* on Long Island (Holden & Qualtrough, 1884). Wragg noted that the *marae* was indeed smaller than that on Nake, with dimensions approximately 3 m wide by 8–10 m long. Its orientation appeared to be northeast-southwest. The wall on one end was evidently smashed by storm waves. Only two of the peripheral upright stones were still standing; they were of similar size to those on Nake. The platform was in reasonable condition, with a huge *Pisonia* tree growing through it. Some rock slabs were large (2 × 2 m). The entire *marae* was situated within a *Pisonia* grove, with some *Cocos* but no *Pandanus* nearby. We do not know if the nearby coconut grove (1.6 ha) was present before 1,343 palms (20% of the islet's area) were planted in 1918–19 (Young, ca. 1922). The sheltered location and a *Pisonia-Cocos* forest, which suggests an old clearing, further indicate prior occupation.

In 1990, G. Wragg also uncovered an RNZAF survey marker just inland of Long's southernmost tip.

Vegetation: There are 15 plant species (4 trees, 2 shrubs, 9 herbs) on Long, 56% of the total flora. Long's variety of habitats, vegetation heights, substrata, and birds make it the most diverse islet on Caroline. Only 3% of its area remains in *Cocos*. All the atoll's seabirds have bred here. Its ecology is best understood with reference to Figs. 35 and 39–41.

Within the basic pattern of five coalesced motus, it may be seen that:

1. From north to south (measured from the midpoint of each former channel) the motus, of divergent size and shape, are approximately 320, 620, 700, 1,840, and 100 m long.

2. Each former islet, crowned by a *Pisonia* forest, contains concentric rings of decreasing fertility around its core and is morphologically similar to islets surrounded by water, except that the coarse coral gravel along the former perimeter is less marked. More specifically, beach sands and gravel extend for 200–300 m north and south of the old channels, after which they increasingly accumulate coral rubble, humus, and guano.

3. The dominant vegetation is *Tournefortia*, interspersed with 4 patches of taller *Pisonia* forest and scattered clumps of *Cocos* and *Cordia*. Interrupted herb mats parallel the windward coast and often extend across the island along former channels (Pl. 33). Vegetation height varies from 2 cm to 15 m.

4. Plant species diversity is highest in *Tournefortia-Pisonia* and lowest in *Pisonia* forests.

5. Long's tallest, most mature *Pisonia* groves (up to 100% *Pisonia*) occur on the largest of the former islets. The *Pisonia* forest near the south end (Tr. 10), although healthy, is only 12 m tall. This may be due to its impoverished *makatea* substrate of pitted reef rock barely covered with "soil." Since it lies adjacent to Long's most luxuriant *Cocos* grove, its land could well have been cleared in 1918–19, with the *Pisonia* forest taking longer than elsewhere to recuperate. Because tern

guano increases soil fertility and is important for *Pisonia* growth (Fosberg, 1953). It is of interest that neither black nor brown noddies nested here.

6. Deep dips in Fig. 39 (lower graph) correspond to east-west corridors formed from old channels. Vegetation in these relatively infertile, sandy flats is low, similar to that on small developing motus (i.e., native herbs with scattered *Tournefortia* <2 m high). One sandy channel (Tr. C; Pl. 33) supported a sparse population of *Suriana*. During the February 1990 cyclone, all vegetation was either uprooted, washed away, or smothered with fresh sand and coral gravel along Trs. A and C (personal observation, March 1990). Storm erosion was particularly marked within the channel that almost bisects the island (Tr. A).

7. Secondary dips mark even older interislet channels ("ancient channels"), visible on aerial photographs (Chapter Frontispiece) but barely recognizable in the field. They are overgrown with *Tournefortia* and/or *Pisonia*.

8. Sharp dips within established forests or herb mats denote relatively recent channels gouged out by storms ("recent storm cuts"). These were also altered during the winter 1990 storm.

Figures 40 and 41 illustrate some differences between the windward and leeward coasts. Transect C (Fig. 40) crosses the north end of Long through an old interislet channel now filled with sand and rubble. Its low profile reflects the simple habitat harboring halophytic herbs and *Tournefortia* shrubs less than 2 m high. Although the shrubs are scattered, the lagoon half of the transect passes through slightly higher ground, which encourages denser *Tournefortia*. This transverse section is similar to that of a formative motu such as Fishball (Fig. 56). This exposed, scrubby swath, 300 m wide, harbors red-footed boobies, great frigatebirds, and a discrete population of masked boobies. Approximately 127,000 pairs of sooty terns nested in a similar sandy channel 740 m to the south (Tr. A, Pl. 59) in 1988.

Transect 8 (Fig. 41) crossed the islet nearer the southern tip (Fig. 8). This profile departs significantly from the usual parabolic cross-section seen on most of the small motus and which exists further north on Long Island. From east (windward) to west, there is first a wide expanse of coarse, unvegetated rubble, followed by rubble dotted with herbs, then *Tournefortia* scrub increasing to 9 m high. Further inland, a forest of 10-m-high *Tournefortia*, *Pisonia*, and *Cordia* continues westward to the lagoon. This leeward margin of Long, extending southward nearly to its tip, is the only location on Caroline where tall, indigenous vegetation overhangs and shelters the lagoon. No herb mat is present.

In summary, Long contains examples of all major plant communities, as well as two minor ecosystems, *Pisonia*–*Cordia* (3.2 ha) and *Cocos*–*Cordia* (0.82 ha). Its woodlands total 49.60 ha. Coconut crabs inhabit all areas containing *Cocos* and *Pisonia*; our rough estimate of their population is 200 crabs.

Birds: In 1988, Long supported 9 (10 in 1965) species of breeding seabirds, as follows (pairs): red-tailed tropicbird (5), masked booby (69), brown booby (12), red-footed booby (659), great frigatebird (808), sooty tern (179,800), brown

noddy (207), black noddy (986), and white tern (751). From 1988 through 1990, sooty terns occupied 19 large colony sites (Fig. 11, Subchapter 1.2).

Comments: Polynesian rats were abundant, especially in *Cocos* and *Pisonia* habitats. It was often possible to see 3 or 4 simultaneously while conducting daily surveys and 20 or more around camp. At night, their numbers increased substantially. Azure-tailed skinks (*Emoia cyanura*) were noted.

Windward Islets

This chain of 13 islets occupies the southern half of Caroline's east coast. All rest on the same reef flat, separated by surge channels varying in width and depth. They can be waded with care at low tides, but most harbor black-tipped reef sharks: up to four were visible in the shallows within 50 m of an observer.

The motus range in size from Noddy Rock (0.02 ha) to Windward (11.42 ha). They support every major vegetation type, from simple herb mats to magnificent *Pisonia* forests, 21 m tall. Because of their constant exposure to trade winds, the seaward vegetation is wind- and salt-shorn. Though appearing completely natural, all of the Windward Islets were intensively planted with *Cocos* (Table 13) from 1916–1920 (Young, ca. 1922). However, these incipient plantations experienced difficulty and appear to have been abandoned within a few years (see Plant Communities section).

Flanking the lagoon of the southern motus (Brothers through Tridacna) and extending westward are coral reefs densely studded with giant clams, whose iridescent, multicolored mantles add to Caroline's outstanding natural assets (Pl. 26; Subchapter 1.2, Conservation section).

3. BO'SUN BIRD ISLET (0.86 ha) (Figs. 29,42; Pl. 9)

We named this motu for its red-tailed tropicbirds, commonly called bo'sun birds. The sizeable population is the largest on Caroline. In addition, our 1988 records constituted the first known breeding of this species on the atoll.

Physiography: Bo'sun Bird Islet, 165 m west of Long's southern tip, is the only motu lying "within" Caroline's lagoon. It shares the same reef as Long, however, and is not a true "lagoon motu."

Amoeboid in shape, Bo'sun Bird is greatly affected by the tidal waters that spread across the shallow reef flats and gush through the surge channels that separate Long and Windward. Because it sits near the inner edge of a wide windward reef flat, the layering of sediments around it is complex and transitory; our observations indicate that more rubble was deposited on the islet's western edge since the aerial photos were taken in 1985. Its western shoreline rises gradually to a high water mark, and slight changes in water level greatly change its overall size and shape. At high tide its perimeter resembles the shape of Pinocchio's head—ovoid with a long, expanded nose. The "head" is approximately 70 m wide and 115 m long, while the "nose" is 45 m long and 15 m wide.

Vegetation and Birds: Bo'sun Bird Islet, composed of coral rubble and sand, supports only natural herb mats (*Heliotropium*, *Portulaca*, *Lepturus*) and *Tournefortia* scrub

(to 4 m tall). These two simple plant communities cover 35% and 55% of the land area, respectively. For its size, the motu is sparsely vegetated, with only four plant species (one shrub, three herbs), 15% of Caroline's total flora. There are no introductions.

Bo'sun Bird's most notable attributes are its 4 species of breeding seabirds: red-tailed tropicbird (47 pairs in 1988, but 130 pairs seen in 1990), sooty tern (8,400 pairs), brown noddy (10 pairs), and white tern (6 pairs).

4. WINDWARD ISLET (11.42 ha) (Figs. 29,43)

We named this "Windward" because it is the first major, and largest, Windward Islet.

Physiography: Windward is broadly crescentic in shape, 508 m long by 287 m wide. It parallels the reef's longitudinal axis and is set close to the lagoon. Its seaward beach is quite narrow (3 m wide); there is no lagoon beach.

Vegetation: Windward has 11 species of plants (3 trees, 1 shrub, 7 herbs), 41% of the total flora. A windward crescent of halophytic herbs borders a zone of *Tournefortia* scrub, which mixes quite densely with *Pisonia* and *Cordia* over most of the interior in a bilobed pattern. These latter forests, reaching 14 m high in the south and 9 m in the north, total 8.67 ha. This unusual distribution of central forests undoubtedly reflects *Pisonia*'s recovery from 100% landclearing for *Cocos*—1,299 palms—in 1920 (Young, ca. 1922, Table 13). It is remarkable that not one *Cocos* remains as a legacy of this disturbance.

The east-west profile of Windward, similar to that of Tr. 8, Long Island (Fig. 41), is typical of most motus, except that lagoon-facing herb flats are almost nonexistent. *Scaevola sericea sericea*, a new plant record for the atoll, is unique to this motu, although *S. s. tuamotensis* was found on South Island in 1990.

Birds: Five species of breeding birds were present, all in appreciable numbers (pairs): red-footed booby (163), great frigatebird (207), brown noddy (20), black noddy (28), and white tern (134).

Comments: In May 1990, AKK noted a possible motu midway between Windward and Crescent Islets during midtide. It appeared to be upraised reef like Noddy Rock, but because of extensive shallow reefs in this area, it has not yet been confirmed.

5. CRESCENT ISLET (3.10 ha) (Figs. 29,43)

We named this islet for its cupped shape.

Physiography: Crescent Islet is 190 m long by 225 m wide. It is almost entirely composed of coral rubble, with a little humus in the interior. The seaward beach is variable (up to 50 m wide), the lagoon beach, insignificant.

Vegetation: There are 10 species (3 trees, 1 shrub, 6 herbs), 37% of Caroline's flora. No introduced plants occur. Plant diversity is poorer than on Windward, a reflection of small size, poor soils, and scant herb mats. However, woodlands cover two-thirds of its area, and the central stand of *Pisonia* and

Cordia is 87 m wide and up to 13 m high. Crescent was heavily planted (80% of total area, 228 palms) in *Cocos* in 1920, but today none remain.

Birds: Crescent Islet was used by the following numbers of breeding pairs: red-footed booby (28), great frigatebird (5), brown noddy (36), black noddy (60), and white tern (8).

6. MOTU ATIBU "Coral Rubble Islet" (0.02 ha) (Figs. 27,43)

Motu Atibu was Caroline's smallest and least vegetated islet. Third in the windward chain, it measured 13 m \times 18 m. We named it for its basic rubble character. Vegetation covered only 2% of the land surface and consisted of a few *Tournefortia* shrubs (<1 m high) encircled by narrow swaths of low herbs and rubble. Its three plant species (one shrub, two herbs)—11% of Caroline's flora—were among the most meager on the atoll. Atibu's profile was similar to that of Fishball (Fig. 56). There were no breeding birds.

Comments: Since a February 1990 storm, Atibu has apparently disappeared, having been reduced to a thin strip of coral gravel below high tide level.

7. NORTH PIG ISLET (5.44 ha) (Figs. 29,44; Pls. 60,61)

We named the fourth windward islet "North Pig" for its location immediately north of Pig Islet.

Physiography: Classically crescentic, North Pig is 350 m long and 230 m wide. Though approximately half Pig's area and less wooded overall, North Pig has a similar distribution of substrates (including sand on the lee side), vegetation, and breeding birds. Profiles of the two motus are nearly identical (Fig. 45).

Vegetation: There are 11 plant species (3 trees, 1 shrub, 7 herbs), 41% of Caroline's flora. No introduced plants are present. Proceeding south along the windward islets, lagoon-side herb mats develop and islet cross-sections assume a more perfect symmetry—low at the edges and forming a hump in the middle.

North Pig's three vegetation zones are predictably symmetrical: a peripheral band of herbs (more extensive on the "horns"), curved belts of *Tournefortia*, and a spacious central forest of mixed *Pisonia*, *Cordia*, and *Tournefortia*. The latter (to 20 m tall) covers more than one-half the islet's width and one-third its area and includes fine *Cordia* groves (Fig. 44). This excellent forest is surprising because 402 *Cocos* palms were planted on 93% of North Pig's usable land in 1920 (Young, ca. 1922, Table 13). Measurements from 25 *Pisonia* trees (main trunks) averaged 19 m in height, 221 cm in circumference (at 1.5 m), and 261 cm in base circumference (Table 12).

Birds: Five species of seabirds bred: red-footed booby (31 pairs), great frigatebird (17 pairs), brown noddy (76 pairs), black noddy (3,199 pairs), and white tern (110 pairs). The largest colony of black noddies on Caroline nested in the tall *Pisonias*.

Comments: Rats and coconut crabs were common.

8. PIG ISLET (7.21 ha) (Figs. 29,44; Pls. 27,41,52,60,61)

Number 5 down the chain, Pig was named prior to 1883. Domestic pigs were introduced to Caroline in 1828 by Captain Stavers but evidently died out before 1834. Reintroduced in 1848 with the first recorded settlers, it is not known how long they lasted. One would expect that they were only on South Island, but the statement that “about one-third the distance up the lagoon a canvas hut exists on one of the smaller islets on the eastern side of the lagoon” (Holden & Qualtrough, 1884) suggests that perhaps domestic animals also inhabited Pig. Though this is weak evidence, there must have been some reason for this curious name. Today, fortunately, no pig devastation is evident here or elsewhere on the atoll.

Physiography: Pig, shaped like a fat kidney bean, is 330 m long and 255 m across. It is separated from North Pig by a channel 60 m wide.

Vegetation: The islet has 11 plant species (4 trees, 1 shrub, 6 herbs), 41% of Caroline’s flora. *Cocos*, the only introduction, is rare (0.03 ha). In 1920, 538 palms were planted (Young, ca. 1922), which covered approximately 79% of Pig’s usable area (Table 13).

Pig’s vegetation profile (Fig. 45) is classic: a wide, windward herb mat, bordered by *Tournefortia* and *Cordia*, which, in turn, grades rapidly into an outstanding *Pisonia* forest (to 21 m tall, 3.36 ha), one of Caroline’s best groves. Measurements from five trees, mostly multiple-trunked, averaged 16 m in height, 338 cm in circumference (at 1.5 m), and 282 cm in base circumference (Table 12). This *Pisonia* also occupies the largest proportion (46%) of any islet area. It is striking that such quality forests could regenerate in about 65 years (see section on Plant Communities, *Pisonia* Forests). In the *Cordia* forest (Pl. 27), also the finest on Caroline, six trees averaged 12.6 m in height, 116 cm in circumference (at 1.5 m), and 99.8 cm around their bases. On the lee side of Pig, *Tournefortia* extends directly to the lagoon shore.

Birds: Five species of seabirds bred: red-footed booby (14 pairs), great frigatebird (118 pairs), brown noddie (82 pairs), black noddie (1,928 pairs), and white tern (164 pairs).

Comments: Rats and coconut crabs were common. In 1990 a grayish gecko (possibly mourning gecko, *Lepidodactylus lugubris*) was seen by A. Garnett.

9. SKULL ISLET (0.02 ha) (Figs. 27,44; Pls. 46,49)

Sixth in the windward chain, we named Skull Islet after finding the skull, tail feather, and eggshell of a red-tailed tropicbird, the first evidence that this species bred on the atoll. A low shelf of coral rubble and sand, barely above high tide mark, this motu is barren except for a small herb mat under five *Tournefortia* bushes (1 m high) on the lagoon side. Only 2% of the surface area is vegetated. There are three plant species (one shrub, two herbs), 11% of the atoll’s flora. Although appearing young, the islet must be more than 100 years old, as it is marked on Arundel’s chart (Fig. 4). After February 1990, several large reef fragments had washed into the channel close to Skull Islet.

In 1988 there were no birds. However, in March 1990, a colony of 150 brown noddies was in a prelaying phase, accompanied by 6 sooty terns, a brown booby and a wandering tattler.

10. NORTHBROTHERS ISLET (1.71 ha) (Figs. 29,44; Pl. 60)

The seventh windward motu, we named this islet North Brothers because of its location directly north of the named motu, Brothers.

Physiography: North Brothers is shaped like an oval that curves lagoonward toward Brothers, 40 m away. The concave shorelines and lack of herb mats on the opposite shorelines of these 2 islets suggest that they might have been formerly connected. Composed primarily of rubbly substrates, with slightly better soils centrally, it is 95 m long and 250 m wide.

Vegetation: Plant species number 10 (3 trees, 1 shrub, 6 herbs), 37% of Caroline’s flora. A few *Cocos* trees are present, remains of the 180 planted in 1920 (Young, ca. 1922), which covered 100% of all available land on the islet (Table 13). Plant communities on North Brothers are simple: *Tournefortia* (more open in the west) rises to an excellent *Pisonia* forest, 80 m wide and 18 m tall, on the east end. Average measurements from three *Pisonia* trees were height 18 m, base circumference 314 cm, and number of trunks, 2.3 (Table 12).

Birds: Five species of seabirds bred on the islet in 1988 (pairs): red-footed booby (25), great frigatebird (9), brown noddie (23), black noddie (40, plus hundreds of old nests), and white tern (69). In September 1989, sooty terns nested on the windward beach (Anne Falconer, personal communication), and in May 1990, a prebreeding swirl of thousands of sooty terns swarmed above Brothers and North Brothers.

Comments: Gecko eggs were seen on *Pisonia* trunks in 1990.

11. BROTHERS ISLET (4.31 ha) (Figs. 29,44,46; Pls. 30,60)

The eighth windward motu, Brothers Islet was named last century after Captain Brothers, who managed a stock-raising venture on Caroline. In 1873, his rights to the atoll passed into the hands of John Arundel.

Physiography: Shaped like a molar tooth, with roots extending toward the lagoon, Brothers Islet lies about two-thirds of the way down Caroline’s windward reef. It is 198 m long × 178 m wide through the center. A *Tridacna* reef extends westward from it almost completely across the lagoon.

An interesting aspect of Brothers’ structure is that Arundel’s chart (Fig. 4) indicates a tiny, separate motu off the southwest point. Our survey and the 1985 aerial photos show that this motu is now joined to Brothers Islet. Its former identity is marked by a small patch of *Tournefortia*, around which the recently deposited sand and rubble is sparsely dotted with native herbs.

Vegetation: There are 11 plant species (4 trees, 2 shrubs, 5 herbs), 41% of Caroline’s flora. *Cocos*, along the leeward shore, is the only introduced plant. Three distinct plant

communities are present: peripheral herb mats (including leeward *Portulaca* with *Suriana*), *Tournefortia* scrub and forest (to 6 m high) bordered with *Cordia*, and a central *Pisonia* forest. Larger trees had up to 15 trunks and multiple root suckers. Measurements of 10 trees (main trunks) averaged 15 m in height, 140 cm in circumference (at 1.5 m), and 243 cm base circumference. Distances to nearest neighbor for 10 trees averaged 4.2 meters. As on its neighbor islets, the *Pisonia* forest on Brothers is striking, especially since it has matured to a closed-canopy monotypic stand devoid of any subcanopy species (Fig. 40), evidently in about 65 years. In 1920, Brothers Islet was planted with 315 *Cocos* palms, which covered approximately 97% of the usable land area (Table 13).

Birds: Four species of seabirds bred: red-footed booby (25 pairs), brown noddy (8 pairs), black noddy (15 pairs), and white tern (50 pairs). In May 1990, large numbers of sooty terns swirled over Brothers and North Brothers Islets.

Comments: Many of the mature *Pisonia* trees contained capacious cavities in their boles that housed large coconut crabs. In March 1990, several of these holes had feathered skeleta of sooty terns (and possibly also brown noddies) outside their entrances, along with freshly-snipped *Pisonia* branches (see Subchapter 1.2, Coconut Crabs section).

12. NODDY ROCK (0.02 ha) (Figs. 27,47; Pl. 19)

We named this ninth motu in the Windward Islets for its only known breeding seabird, the brown noddy. In September 1988, at least 80 pairs were incubating their eggs on the *Portulaca* mat that covers its central lee section.

Noddy Rock, an eroded limestone plateau (*feo*), is 26 m wide by 9 m long. It is windswept and salty, with waves splashing over its eastern edge on most days (it rises only 0.5 m above high water). During storms it is completely awash (Anne Falconer, personal communication). Only three species of plants (11% of Caroline's flora) grow here, thinly covering the western (leeward) third of the island in the following proportion: 75% *Portulaca*, 20% *Lepturus*, and 5% *Tournefortia*.

13. NORTH ARUNDEL (0.91 ha) discussed below (Figs. 29,34,47; Pls. 14,62)

14. ARUNDEL (7.34 ha)

Arundel Islet was named last century in honor of John T. Arundel. A British trader and guano digger, Arundel was one of the leading figures in the Pacific phosphate industry, directing guano and coconut planting operations on Caroline and other islands from 1873 to 1897. His most valuable contributions, however, were his excellent surveys and maps of several central Pacific islands, including Caroline (Fig. 4). The islet immediately to its north, Arundel's "cap," we named North Arundel.

Physiography: Arundel's shape is a fat crescent, with wedge-shaped North Arundel lying across a short channel immediately to its north. North Arundel is 80 m long × 130 m

wide, while Arundel is 375 m long × 210 m wide. They are composed almost exclusively of coral rubble and flanked on their inner edges by *Acropora* reefs heavily laden with *Tridacna* clams. Arundel's inner "horns" have evidently added more sand and rubble since 1883 (Fig. 4).

Vegetation: There are 11 plant species (3 trees, 1 shrub, 7 herbs) on Arundel, 41% of Caroline's total. There are no introductions. North Arundel has 11 (4 trees, 1 shrub, 6 herbs), 41% of Caroline's flora, including one introduction, *Cocos*.

The vegetation on this pair of motus, along with *Tridacna* to the south, consists of extensive herb mats, low scrub and small interior forests (Fig. 34), slightly less lush than the more northerly windward motus. Their woodlands are primarily *Tournefortia*, with a thin belt of *Cordia* and central *Pisonia* groves (a bilobed pattern on Arundel). *Morinda* is unusually common in Arundel's central forests, and *Achyranthes* is especially abundant on North Arundel. *Pisonia* occupies only 13% of the land area on Arundel, compared to 46% on Pig. Soils are extremely rubbly, with scant organic matter, a possible legacy of the guano era.

Both North Arundel and Arundel were heavily planted with *Cocos* in 1919–20 (69 and 646 palms, respectively). All usable land was cleared (Table 13). Despite the extreme paucity of *Cocos* today, the relatively scant *Pisonia* present today on these islets, compared to those further north, suggests that the *Cocos* plantations were more successful here. Their proximity to South probably also guaranteed better maintenance.

Birds: Five species of seabirds bred on Arundel: red-footed booby (37 pairs), great frigatebird (on territory, September 1988; breeding confirmed, early 1989 by Anne Falconer), brown noddy (11 pairs), black noddy (249 pairs), and white tern (227 pairs). In May 1990, thousands of sooty terns swarmed above Arundel and North Arundel.

15. TRIDACNA ISLET (9.08 ha) (Figs. 29,48,49; Pls. 1,26,48,62,63)

The 13th and southernmost motu in the windward chain was named by the present authors and Boris Sirenko for its outstanding coral reef studded with giant clams (*Tridacna maxima*).

Physiography: Somewhat crescentic, measuring 446 m long and 250 m wide, *Tridacna* is one of the largest motus on Caroline. Its ground surface is heavily littered with coral rubble, having a sandy strip above the beach crest on the windward edge.

Vegetation: There are 13 plant species (2 trees, 2 shrubs, 9 herbs), 48% of the atoll's flora. For its size, *Tridacna*'s vegetation is surprisingly lacking in tall forests, a legacy of the 910 *Cocos* palms planted on 82% of its available land area (Table 13). Vegetation patterns follow the usual concentric zonation: peripheral herb mats border a discontinuous belt of *Suriana* (windward side), while the large central mass is dominated by scrubby *Tournefortia*–*Morinda* woodlands, which cover 88% of the islet's area, yet only attain 7 m in height. In cross-section (Fig. 49), the short woodlands are particularly noticeable. Compare the present lack of *Cordia*,

paucity of *Pisonia*, and richness of herbs, both in species numbers and abundance, with Pig (Fig. 45) and Brothers (Fig. 46). Although there are no introduced plants, thick patches of *Lepturus* also reflect past forest clearing.

Birds: Four species of seabirds were nesting in 1988: red-footed booby (111 pairs), brown noddy (11 pairs), black noddy (249 pairs), and white tern (227 pairs). *Tridacna* is periodically a major breeding area for sooty terns. Clapp & Sibley (1971a) found 4 main colonies totaling 250,000 birds, and large numbers nested along the windward beach in August 1989 (A. Falconer, personal communication). Nests were located under shrubs, or in open areas bordering them, and were evidently preyed upon by coconut crabs.

16. SOUTH ISLAND (104.41 ha) (Figs. 30,36,50; Pls. 1–7,12,16,24,34,39,44,45,50,62)

History: The history of South Island (called Rimapoto in Young, ca. 1922) is essentially the history of Caroline, for most information about the atoll prior to 1965 is from here. It is the second largest islet, and the staging area for trips up-lagoon as it lies adjacent to both the “boat landing” and “blind passage.”

South Island was inhabited in prehistory by Tuamotuans, who planted the first small coconut grove on its northwest point. The first Europeans to land, in 1606, found coconuts, fish, lobsters, and seabirds in abundance. They dug for fresh water in vain. Two hundred years later, in the decade after a cyclone in 1825, pigs, sweet potatoes, arrowroot, and South Sea chestnut were introduced. However, “the unfriendly character of the soil, and the number of land crabs that infest it, gave us but little hope of the experiment succeeding” (Bennett, 1840). The pigs expired within a few years. The arrowroot, tenacious and adapted to island environments, still exists today (unless later immigrants brought it). Of the others—plus many other later food plants and ornamentals—no trace exists (Table 1). (In 1990, we found a few *Hibiscus tiliaceus*, *Thespesia populnea*, and *Ximenia americana*. All could be indigenous. The first 2 species were often planted by Polynesians in copra-cutting settlements [e.g., Flint Island]). Tropical heat, droughts, storms, excessive shade from *Cocos*, poor germination, poor soils, terrestrial crabs, and lack of care all undoubtedly contributed to their demise.

The first recorded settlement on Caroline, and first for the Line Islands, was in 1846, on the northwest point. These settlers, as well as subsequent ones, eked out a spartan living by raising stock, drying fish and copra, and digging for guano. Their managers built “proper” dwellings, so when US, British, and French astronomers arrived to observe the solar eclipse in May 1883, South Island was quite “civilized,” far more than it is today. Three houses and two sheds “were in good repair,” and a variety of “anchors, chains, spars, and pieces of the woodwork of vessels” littered its reefs (Holden & Qualtrough, 1884). Large grassy clearings adjacent to the lagoon accommodated several European-style houses (Pls. 2–4). The astronomers’ account of South Island, illustrated with pen-and-ink drawings (Pls. 2–5, 50), is the only record of buildings on Caroline, apart from mention of perhaps the same dwelling, the manager’s house, reported in 1936 by the “H.M.S.”

Wellington to be “in excellent condition and spotlessly clean” (Maude, ca. 1938), and a copra shed seen by Clapp & Sibley (1971a). Arundel also took photographs, including some of the *marae* on Nake, which we have not examined (Arundel’s memorabilia [photos, letters, diaries, a microfilm, et cetera] are deposited in the Rare Book Collection, National Library and Pacific Manuscripts Bureau, Research School of Pacific Studies, Australian National University, both in Canberra, A.C.T., Australia).

Today, the houses, sheds, brick piers (constructed in 1883 for telescopes and observatory frames), signboard, flagpole, marble slab with inscription “U.S. Eclipse Party, 1883, May 6,” and all but one of the introduced plants have disappeared. In three trips we found no traces of the copra shed, nor have the Falconers, after repeated visits over 2 years. All that remains of the formerly large clearings are two small palm-shaded “flats,” in 1988 used by the US and Soviet scientists for a base camp and work area. In 1987, the Falconers cleared one of these for living quarters, and in 1990 fishermen expanded the other by burning an area 35 × 22 m, then erecting a tin shack, cookhouse, and fishtrap, which were destroyed in a summer 1990 storm.

Our “civilization list” probably covered all that could be seen on South Island without digging: a 26-foot wrecked sloop (AK 6691 J.), complete with trail to a “Robinson Crusoe-type” campsite strewn with remnants of radio and navigational equipment, sail, cans, clothing, et cetera (southeast coast); assorted flotsam and jetsam (whisky bottles, Japanese fishballs, plastic debris, et cetera); a large rubber ship fender; a bench mark from the 1985 RNZAF survey team; a recently renovated concrete cistern (by the landing); and an old wooden canoe lying on its side just like de Quiros found in 1606!

We assume that all the Polynesians, ancient and recent (Tuamotuans, Tahitians, Niueans as far as is known), lived in native thatched huts similar to the ones on Ana-Ana today. Fashioned from coconut palms and pandanus trees, they disappear quickly when abandoned. The largest number of inhabitants recorded for Caroline (probably all on South Island) was “two managers and 52 laborers” in 1873 (The Commercial Advertiser, 1873).

The history of South Island’s coconut plantations from 1885 to 1901 and from 1916 to 1929 is discussed under Coconut Woodlands (Plant Communities section).

Physiography: South Island forms the base of the thinly crescentic isosceles triangle whose limits define the atoll. Its own shape is that of an irregular parallelogram 858 m wide × 1,254 m long at its longest points (Fig. 50). The north coast, a curved bay, forms the lower boundary of the lagoon. This shore, along with the adjacent northwest peninsula, has been the most trodden by man, but the scars have healed, leaving few traces beyond the presence of coconut palms.

The reef flats surrounding the outer three sides of South are the widest on the atoll, averaging 231 m, 578 m, and 363 m on the east, south, and west, respectively. The windward and leeward reefs immediately to its north are 530 m wide. To leeward is the small boat “landing,” and to windward, the “blind passage.”

Aesthetically, the lagoon fringe is one of the most picturesque spots on the atoll. Lush palms overhang a narrow beach of blinding white sand and coral gravel, affording idyllic views of the azure lagoon and its encircling wooded motus (Pls. 7,24,39).

Vegetation: There are 23 plant species (7 trees, 3 shrubs, 13 herbs), 85% of the atoll's flora. *Cocos* dominates South Island, occupying 77% of its area. The healthy, but old, closed-canopy plantations (21 m tall) that border its coastlines give no indication of the vast extent of the overgrown, dying groves that occupy two-thirds of its interior (Fig. 50; Pls. 7, 34). Here, three species of herbs (*Boerhavia repens*, *Portulaca lutea*, *Phymatosorus scolopendria*) have proliferated unnaturally to form dense carpets, and the vine *Ipomoea macrantha* climbs, in tangled, strangling masses, to the tops of the highest palms.

The natural communities that prevail on other motus are only minor components on South (Fig. 50): herb mats (13% of the total area), coastal scrub with *Suriana* (1%), and *Tournefortia* scrub (4%). Conspicuously absent are prime scrublands and forests of *Tournefortia*, *Pisonia*, and *Cordia*, which undoubtedly once swept in a lush expanse from shore to shore, stratified and zoned as on other motus. Canopy heights of the plantations are uniform (21 m), and the outer fringe of indigenous scrub (*Tournefortia*, *Cordia*, *Suriana*) and herbs (*Heliotropium*, *Portulaca*) occupy a small proportion of the island's width (Figs. 36,51). Note the abrupt transition of canopy heights as they drop to the level of coastal scrub on both sides of the plantation (Fig. 51). *Pandanus*, too, is less extensive than formerly: Bennett (1840) called *Pandanus* "somewhat numerous" and Pl. 50 reproduces an 1883 painting of a grove, denser than any existing today on South. During our survey, we observed only one small *Pandanus* grove and a few scattered trees. Bennett also noted that the island was "covered with verdure," and there were "trees attaining the height of twenty feet." However, it is well to recall that 9 or 10 years previous to Bennett's visit a violent storm had whipped over the atoll. Drawings from 1883 (Pls. 4,5) depict remnant *Tournefortia* and *Pisonia* trees larger than this.

Apart from the coastal buffer zone, little native forest remains. Other sizable trees (*Pisonia*, *Cordia*), up to 17 m tall, are rare, but *Morinda*, tolerant to both sun and shade, is still quite common. Though we have not been able to trace any records to Caroline, it is possible that shiploads of *Cordia* logs were exported to San Francisco on guano ships, as was the case on Flint, worked simultaneously by Arundel's company (Young, ca. 1922).

A final noteworthy aspect of South Island is that, despite its history of sporadic occupation and extensive forest felling for coconut plantations, only one "weed," a tiny patch of *Phyllanthus amarus*, and no vegetable or garden ornamentals (excluding Polynesian introductions) have survived. (We are unsure of the status of *Hibiscus tiliaceus*, *Thespesia populnea*, or *Ximenia americana*). The 19th century gardens, once drenched in sunshine, have long been buried beneath the deep shade of palm groves (compare Pls. 2 and 24). In addition, periodic storms, droughts, irregular rainfall, nutrient-poor soils, rats, land crabs, and the harsh salty environment must have contributed to the eradication of all exotics except traditional

native food and medicine plants, which are specifically adapted for atoll environments. Studies on other atolls, even those near high islands (Stoddart & Fosberg, 1972; Stoddart & Gibbs, 1975), have demonstrated also that exotics survive, despite the proximity to source areas containing garden ornamentals and weed plants. We learned on our last two visits (March and May 1990), however, that a small sunny clearing around the cistern has attracted one clump of a weed not previously reported (*Kyllinga brevifolia*), also the location of *Phyllanthus*. This area is now used as an extension of the Falconers' vegetable garden on Motu Ana-Ana. *Kyllinga* is listed as a temporary species (Table 1).

Birds: Only 2 species of birds bred on South in September 1988, a reflection of its paucity of natural habitats: brown noddy (163 pairs) and white tern (381 pairs). Bristle-thighed curlews are very common, gathering in small flocks on the rubbly shores (Subchapter 1.2, this volume). They also forage in the open *Ipomoea*-*Cocos* forest, perching on dead coconut stumps 6-10 m high, then flying down to feed in the thick herb mats.

Terrestrial Crabs: Caroline's highest population of coconut crabs, having many huge individuals decades old, occupies the open *Cocos* forests (Pls. 22,56,57). A crude minimum estimate for South Island is 500 mature individuals (since March 1990, these have become much reduced due to killing and preserving in formalin for curios). We also found a fist-sized blue hermit crab within a *Turbo* shell, possibly *Coenobita brevimanus* (Yaldwyn & Wodzicki, 1979; E. Reese, personal communication). As elsewhere on the atoll, land crabs such as the reddish-purple *Cardisoma* sp. and scarlet hermit crabs, *Coenobita perlatus* (in *Turbo argyrostomus* shells), were abundant (Pl. 38). A *Geograpsus* sp., closer to the shore, was less common.

Rats: Polynesian rats were abundant on South, active both day and night. The rats were constantly afoot in broad daylight, and at night a small flashlight beam often revealed a half dozen at a time.

South Naked Islets (Fig. 52)

This chain of seven islets extends 1,500 m south from Naked on the west side. They range in size from 0.64 ha (Kota) to 7.36 ha (*Pandanus*). All are well wooded and support every natural plant community. Proceeding south, the overall plant cover thins somewhat, but not to the dryness and openness of the Central Leeward Islets. The herb mats are more extensive than on the windward islets, especially to seaward. Aboriginal introductions (*Cocos*, *Pandanus*) are sparse. We have found no historical records indicating human disturbance to these islets, thus their vegetation, with the possible exception of *Pandanus* Islet, is evidently natural. The two scrawny *Cocos* are probably drift-derived.

On the Solar Eclipse Party's map of Caroline (Fig. 5), only the top two islets of this group are drawn. The South Naked Islets constitute the only cluster of motus that show appreciable differences between Arundel's chart (Fig. 4) and the 1985 aerial photos: most were shown as smaller, and with slightly different shapes, by Arundel. The interior vegetation on these motus includes mature forests of *Tournefortia*, *Pisonia*, and

Pandanus, so it is unlikely that these differences reflect changes to the center of the motu. However, since the islets now appear larger, accretions of coral rubble and sand that may have occurred in the past 105 years, and are now barren or covered only with herb mats, could account for most of the differences (see Coral Islet discussion).

Although we have no actual records of sooty tern colonies on this chain of islets, in May 1990 AKK observed pre-breeding swirls of this species over Lone Palm, Kota, and Mouakena (Subchapter 1.2, Fig. 11).

17. PANDANUS ISLET (7.36 ha) (Figs. 29,52; Pl. 64)

This motu was named by the present authors for its coastal *Pandanus* grove, probably a drift-derived offshoot from a parent colony on Nake.

Physiography: Pandanus Islet, first in the chain, is irregularly oval, 400 m long and 258 m across. It is nearly twice the size shown on Arundel's map (ca. 3.4 ha). It occupies a sheltered spot at the apex of the lagoon. Sand, actively filling in the adjacent lagoon, is an important component of the substrate on Pandanus, extending one-third of the way across the islet. Although tidal reef flats are absent on the lagoon edge, they average 75 m wide on the seaward side, producing a fairly high proportion of rubble compared to the total land surface (32%).

Vegetation: Plant species total 10 (3 trees, 1 shrub, 6 herbs), 37% of Caroline's flora. *Cocos*, surprisingly, is absent, despite the close proximity to Nake. Pandanus Islet has four basic vegetation zones: natural herb mats, *Tournefortia* scrub (with *Pandanus*), *Tournefortia*–*Pisonia* forest, and pure *Pisonia*. Woodlands cover 62% of its area. The widest pioneer mats (13 m) of any leeward motu occupy its east edge and though sparsely vegetated (20% *Heliotropium*, 5% *Lepturus*, 5% *Portulaca*) reflect active growth toward the lagoon. Proceeding west across the island, *Tournefortia* scrub (2 m high), with pockets of pure *Pandanus* (10 m high), merges into *Tournefortia*–*Pisonia* forest (to 14 m high), whose bimodal distribution suggests that the islet was once divided. The seaward coast supports open *Tournefortia* (5 m high), beneath which herbs eventually thin out onto the extensive reef flats.

Birds: Five species of seabirds breed: masked booby (2 pairs), red-footed booby (32 pairs), great frigatebird (26 pairs), brown noddy (26 pairs), and white tern (52 pairs).

Comments: Skinks and rats were observed, along with the ubiquitous *Coenobita* and *Cardisoma* crabs.

18. DANGER ISLET (2.71 ha) (Figs. 29,52; Pl. 65,68)

We named Danger Islet to commemorate the deep, shark-infested channel to its north, a barrier that aborted our first (dusk) attempt to survey the South Nake Islets.

Physiography: Danger, shaped like a thickened comma, is approximately 150 m long and 215 m wide. It is composed almost entirely of coral rubble; interior humus is scant. Its reef-channel flats are 21 m (north) and 14 m (south) wide. The east

and west beaches, narrow and wide respectively, are typical of all the leeward motus.

Vegetation: Danger has 10 plant species (3 trees, 1 shrub, 6 herbs), 37% of the total flora. There are no introductions. The usual concentric vegetation is clearly zoned: herb mats, *Tournefortia* scrub and forest, central *Pisonia*, and *Cordia* in the southwest. The herb mats are wide, extending 22 m and 15 m on the north and south shores, respectively.

Birds: Four species of nesting seabirds were present in 1988: red-footed booby (139 pairs), great frigatebird (26 pairs), brown noddy (26 pairs), and white tern (52 pairs).

19. BOOBY ISLET (0.84 ha) (Figs. 29,52; Pl. 66)

We named this motu, third in the chain, for its two species of boobies, the common red-footed and rarer masked booby.

Physiography: Booby, shaped like a teardrop, is 70 m long and 125 m wide. Its coral rubble flats extend 10 m and 30 m on the north and south sides, respectively.

Vegetation: Despite its small size, the most notable feature of Booby is its *Pisonia* forest, 20 m tall and undoubtedly virgin. It occupies the exact center of the islet in a circle about 40 m in diameter. Surrounding this is *Tournefortia* scrub (to 8 m tall), thinning out to peripheral bands of coral rubble. Although less than one hectare in size, Booby Islet's woodlands occupy two-thirds of this area. Booby Islet has nine species of plants (two trees, one shrub, six herbs), 33% of Caroline's flora, and no introductions.

Birds: Five species of seabirds breed: masked booby (7 pairs), red-footed booby (52 pairs), brown noddy (2 pairs), black noddy (1 pair), and white tern (6 pairs).

20. CORAL ISLET (1.70 ha) (Figs. 29,52; Pl. 66)

Fourth from the north, Coral Islet was named for its reef-derived coralline substrate.

Physiography: Shaped like an arrowhead, Coral is approximately 130 m long by 200 m wide, more than three times the size mapped by Arundel (Fig. 4). Most of its area is barely higher than the surrounding interislet channels. The shallow reef flats between Coral and its two southern motus are only several centimeters deep at low tide; all three may be destined to unite. Unless closely inspected, they appear to have already merged, a fact which, together with Bryan's incorrect map (Fig. 6), helps account for the widely differing number of motus attributed to Caroline.

Vegetation: There are nine species of plants (two trees, one shrub, six herbs), 33% of Caroline's flora, and no introductions are present. Plant communities comprise a small *Pisonia* forest (0.13 ha), which is surrounded by the predominant *Tournefortia*, which in turn is fringed with a narrow band of native herbs. "Soils" are extremely coarse.

Birds: Five species of seabirds bred in 1988: masked booby (1 pair), red-footed booby (28 pairs), great frigatebird (2 pairs), brown noddy (6 pairs), and white tern (15 pairs).

21. LONE PALM ISLET (1.99 ha) (Figs. 29,52; Pls. 66-68)

We named Lone Palm, fifth in the chain, for its single coconut palm, which towers, flag-like, above a dense mound of *Tournefortia*.

Physiography: Similar to Kota (to its south), Lone Palm is sausage-shaped, 97 m long and 240 m wide, and four times the size mapped by Arundel. Although composed almost entirely of coral rubble, some sand borders the lagoon. Following a pattern prevalent on all the leeward motus, its lagoon beach is 2 m wide, while the seaward beach is 17 m.

Vegetation: Eleven species of plants are present (three trees, one shrub, seven herbs), 46% of Caroline's flora. Lone Palm's plant communities are simple: a wide band of herb mats and open *Tournefortia* flanks an oval of *Tournefortia* forest (to 10 m tall). A line of *Pisonia* trees, with a lone *Cocos* surmounting the scrub, easily identifies this islet from lagoon or ocean.

Birds: Three species of seabirds bred in 1988: masked booby (2 pairs), red-footed booby (48 pairs), and white tern (9 pairs). In May 1990, we saw a large prebreeding swarm of sooty terns.

22. MOTU KOTA "Red-footed Booby Islet" (0.64 ha) (Figs. 28,52; Pls. 66,68)

We named this motu for its high density of red-footed boobies (*kota* in Gilbertese).

Physiography: Sixth in line south of Nake, sausage-shaped Motu Kota is 50 m long and 175 m wide. At low tide it is almost connected to Motu Mouakena. Both surveys indicate that coral rubble, the islet's predominant substrate, had further accumulated on its south side since the 1985 aerial photos and also since 1988.

Vegetation: Though barely wooded, Kota has 11 species of plants (3 trees, 1 shrub, 7 herbs), 41% of Caroline's flora. One introduction is present, a single, tattered *Cocos*, partly hidden by vegetation. Two plant communities are present: peripheral herb mats and central *Tournefortia* scrub (to 10 m tall), with a few *Pisonia*.

Birds: Three species of seabirds bred in 1988: brown booby (1 pair), red-footed booby (12 pairs), and white tern (3 pairs). In May 1990, a single masked booby was on territory, and sooty terns swirled overhead.

23. MOTU MOUAKENA "Masked Booby Islet" (1.00 ha) (Figs. 29,52; Pls. 15,69)

This islet was named for its nesting masked boobies, a relatively uncommon seabird on Caroline.

Physiography: Somewhat U-shaped, Motu Mouakena is seventh, and southernmost, in the South Nake chain of islets. Both sides of the "U" were, in the recent past, separate islets. By joining on the west, a narrow, V-shaped inlet was created on the lagoon side. Motu Mouakena, 100 m long and 160 m wide, is extremely rubbly and infertile; much rubble was reorganized during the February 1990 storm. Seventeen meters to its south lies a newly emerging shoal of sand and gravel (Pl. 15), perhaps destined to be Caroline's fortieth motu or perhaps part of

Mouakena's southern shore. Since the above storm, rubble has further accumulated on this shoal, its adjacent reef flats, and the channel separating it from Mouakena. It already supports one *Tournefortia* shrub, two dozen *Heliotropium* plants, and very scattered *Lepturus* and *Portulaca*.

Vegetation: The number of species is eight (one tree, one shrub, six herbs), 30% of Caroline's flora, with no introductions. Mouakena is thinly vegetated with open *Tournefortia* scrub (to 9 m tall, 26% cover), a few small *Pisonia*, and very sparse herb mats.

Birds: Mouakena has less vegetation and fewer birds than might be expected from a consideration of its area because much of it is unshaded, coarse coral rubble. Though unproductive botanically, this provides ideal nesting grounds for masked boobies, one of the two species of breeding seabirds on the islet in 1988: masked booby (3 pairs) and red-footed booby (8 pairs). In May 1990, we saw one great frigatebird nest with eggs and a swirl of sooty terns.

Central Leeward Islets

This chain of 11 motus occupies the central west side of Caroline. All are separated by channels, wadable only at low tide but prowled by belligerent sharks. Approximately 1,600 m south of Motu Mouakena lies a sandy shoal (0.5 m high, 7 m wide, 4 m long), close to the lagoon edge of the reef flats and connected only by a thin thread of rubble to Motu Mannikiba to its south.

The islets range in size from Mannikiba (28.50 ha), the most northerly, to Fishball (0.46 ha), the most southerly. All support good seabird populations and, though quite well wooded, are nonetheless the least lush motus on Caroline. Historical records of the Central Leewards are very scant: much of Mannikiba's forest was felled to make room for a *Cocos* seedling "nursery" (Young, ca. 1922). The bulk of "40 trees on other islets," in Young's totals, were most likely from Shark and Emerald. The rest of this group is evidently pristine; the natural communities on Bird Islet, in particular, are in excellent condition.

Shark Islet boasts the best sandy beach on the atoll. In common with all the motus on Caroline's west rim, their lagoonside beaches are narrow and leeward reef flats wide. The leeward flats are composed of a greater variety of substrata than the former, including coral rubble of several grades (always gray), upraised reef, and beachrock. Periodically, thousands of nesting sooty terns occupy their open spaces (Clapp & Sibley, 1971a; AKK, personal observation; Anne Falconer, personal communication).

24. MOTU MANNIKIBA "Seabird Islet" (21.49 ha) (Fig. 29; Pls. 70-72)

We named this motu for its teeming seabirds, *mannikiba* in Gilbertese.

Physiography: Largest and most northerly of the Central Leeward Islets, Mannikiba is somewhat rectangular with rounded corners. Its reef flats, containing an incipient islet, stretch 2.0 km north to the South Nake Islets.

Mannikiba's maximum dimensions are 700 m long and 375 m wide. On the lagoon side, the scrub skirts high water, but when the tide drops, a strip of blinding white sandy coral lines the lagoon. To seaward, upraised reef, beachrock, and successive layers of gray coral rubble stretch in a wide swath (40 m) toward the outer reef, 130 m distant. Throughout the islet the substratum is gray coral rubble, with some exposed reef flat hardpan in the northeast. Having numerous seabirds, this motu might have also contained productive guano deposits.

Vegetation: Mannikiba, the fourth largest motu, harbors 13 plant species: (4 trees, 2 shrubs, 7 herbs), 48% of Caroline's flora. One of its shrubs (Species A), a new record for Caroline, has yet to be identified. The only introduction is *Cocos*, occupying 0.1% of the land area.

Mannikiba's vegetation, denser toward the north end, is clearly zoned: herb mats, *Tournefortia* scrub and forest, and scattered *Pisonia* groves. The few clumps of peripheral *Cocos* are probably not drift-derived but the remnants of 6,000 "seed sets" brought from Flint Island in June 1920. These were stored on Mannikiba and "used to replant misses on other islets" (Young, ca. 1922).

Pisonia, though present, occupies only 5% of the land area, a small percentage for such a large islet. This suggests that a large portion of the interior forests were felled to accommodate the coconut "sets." This is also confirmed by the presence of several old cut stumps in the interior. A century ago, Holden & Qualtrough (1884) noted that "About one-third the distance up the lagoon a canvas hut exists on one of the smaller islets on the eastern side of the lagoon, and two wooden huts stand on one of the western islets, some distance further up the lagoon." Mannikiba, the largest western islet, situated about halfway up the lagoon, was most likely the site of the wooden huts, erected around 1920 and used for the following few years when the new company, S. R. Maxwell & Co., Ltd., was anxious for the success of Caroline's plantations. Although nothing more is known of Mannikiba's history, collection of guano from its numerous seabirds, including large populations of frigatebirds and sooty terns, may account for further past disturbance.

Transect 1 (north-central sector, Pl. 71) passed through the heart of a fine interior forest, while Tr. 2 (south-central sector) passed through scrub and herb mats, which may represent part of the former *Cocos* "nursery." Profiles through these two cross-island transects resemble those from Brothers (Fig. 46) and an old interisland channel on Long (Fig. 40), respectively.

The low, peripheral herb mats (absent from the lagoon side) are composed of 30% *Heliotropium*, 20% *Boerhavia*, 15% *Tournefortia*, and less than 1% of *Portulaca* and *Laportea*. They are best represented in the southern sector. The *Tournefortia* forest, 6 m high on both sides, is thick, having 95% canopy coverage. The *Pisonia* forests, though fragmented (12 m high, 100% canopy cover), contain *Morinda*, *Boerhavia*, *Achyranthes*, *Laportea*, and *Phymatosorus*, but none cover more than 10% of the ground area.

Seabirds: Six species of seabirds are known to breed: red-footed booby (184 pairs), great frigatebird (287 pairs), brown noddy (161 pairs), black noddy (176 pairs), and white tern

(195 pairs). No sooty terns nested on this islet in 1988, but Clapp & Sibley (1971a) estimated 2,500 pairs in 1965, and the Falconers reported large colonies on Mannikiba, Blackfin and Matawa in July–August 1990.

Comments: Coconut crabs live in the *Cocos* grove. Azure-tailed and snake-eyed skinks (*Cryptoblepharus poecilopleurus*), as well as a gecko, were noted in 1990 (DHE, G. Wragg, personal observation).

25. BLACKFIN ISLET (2.62 ha) (Figs. 29,54; Pls. 31,73)

We named this motu, second in the Central Leeward chain, for two exhilarating shark attacks (near misses) within its northern surge channel.

Physiography: Blackfin, shaped like conjoined ovals, is 140 m long and 190 m across. Coral rubble covers 30% of its surface; all beaches and upper reef flats are of variable widths, due in part to the fact that it has, in the recent geological past, incorporated a smaller, circular motu into its northern confines.

Vegetation: Blackfin Islet has nine species of plants (three trees, one shrub, five herbs), 33% of Caroline's flora. The only introduction, *Cocos*, is rare. Four plant communities were identified. Herb mats are well represented, especially around the newly incorporated islet. The *Tournefortia* scrub, 21 m wide in the east, is short (to 2 m), but approaches the stature of a forest (to 6 m) in the west. The central forests of *Cordia* and *Pisonia* (0.41 ha) are 9 m high.

Birds: Three species of seabirds bred in 1988: great frigatebird (4 pairs), brown noddy (37 pairs), and white tern (11 pairs). In May 1990, one red-footed booby sat tight on a nest, while two months later large numbers of sooty terns began laying.

26. MOTU MATAWA "White Tern Islet" (1.71 ha) (Figs. 29,54; Pl. 55; Subchapter 1.2, Pl. 3)

On arriving at this islet, the authors were swarmed by 15 white terns, all hovering within arm's reach and exhibiting the ethereal grace that inspired their former common name, fairy tern. I-Kiribati (Gilbertese) call them *matawa*.

Physiography: Of oval shape, Motu Matawa is third from the north in the Central Leeward chain. It is 105 m long and 190 m wide. The entire motu, like all of Caroline's small to medium islets, is built of coral rubble of varying grades, whose unvegetated portion comprises one-fourth or more of the land area. Its lagoon beach is 2.5 m wide, while the seaward beach (sparsely vegetated) is 6 m wide.

Vegetation: Matawa has 10 species of plants (4 trees, 2 shrubs, 4 herbs), 37% of Caroline's flora. There are no introductions. The usual plant communities were present, dominated by *Tournefortia* (to 7 m), which covers half the islet. Vegetation is less lush and more open as one progresses south on the leeward side. Coral rubble, flanking the beaches and extending further inland, also becomes more evident. The east-central *Pisonia*–*Cordia* forest (to 8 m) rises barely higher than its surrounding *Tournefortia*.

Birds: Four species of seabirds bred: red-footed booby (5 pairs), great frigatebird (1 pair), brown noddies (3 pairs), and white tern (13 pairs). Most conspicuous were white terns, with 9 pairs breeding on the 30-m-wide transect swath. One dark morph reef heron fished in the shallows. In summer 1990, sooty terns bred.

27. EMERALD ISLE (8.34 ha) (Figs. 29,54; Pls. 25,74–76)

Fifth down the chain, we named Emerald for the richly colored, translucent lagoon waters that fringe its shorelines.

Physiography: Of thickened crescentic shape, Emerald is 330 m long and 240 m wide. Its lagoonside reefs, patch reefs, and coral knolls are irregularly patterned with sandy channels. It is here that the verdure of the lagoon is most intense.

Vegetation: Emerald Isle has 12 species of plants (5 trees, 1 shrub, 6 herbs), 44% of Caroline's flora. The only introduction is *Cocos*. Four plant communities, with a fairly high species diversity, are present: the herb mats, covering one-fourth of its land area, are composed almost exclusively of *Heliotropium* (35% cover) with scattered low *Tournefortia* (30% cover). The *Tournefortia* scrub and forest attains a maximum height of 8 m and, for a little variety, is mixed about equally with *Pandanus* over most of its width (144 m) on the seaward side.

The interior forest (to 11 m tall) is also mixed, with *Pandanus*, *Tournefortia*, *Pisonia*, and a little *Cordia* (Pl. 75). This condition is similar to the mixed forest on Nake, but because *Cocos* is absent, it appears more natural. The existence of this 3.20 ha mixed forest, as well as a similar one on Shark, prompted us to suggest that *Pandanus* may be both native and Polynesian-introduced. *Cocos* is present as two small groves, complete with coconut crab sign (mounds of shredded fibers, Pl. 57), beside the east and midwest shores.

We have been unable to trace the history of Emerald's forests; the presence of *Cocos* on the west side and fragmented *Pisonia* suggest past disturbance.

Birds: Six species of breeding seabirds were present: red-tailed Tropicbird (1 pair), red-footed booby (3 pairs), great frigatebird (230 pairs), brown noddies (7 pairs), black noddies (150 pairs), and white tern (83 pairs).

Although we did not locate any red-tailed tropicbird nests, two adults circled steadily overhead. Two reef herons (one dark morph, one light) also foraged in the inshore reef shallows.

28. SHARK ISLET (7.98 ha) (Figs. 29,55; Pls. 29,77)

We named this islet to commemorate a particularly pugnacious shark who was so anxious to procure a human foot that it charged shoreward and leaped up onto the beach.

Physiography: Stoutly crescentic, Shark Islet is 280 m long and 310 m wide in the center. The sandy lagoon beach and rubbly seaward beach are each 3 m wide. Beyond high water the seaward reef flats extend for 280 m. Like Emerald, Shark's reefs and surrounding lagoon waters reflect particularly stunning colors, perfect complements to the sparkling pink coral sand of Caroline's prime beach.

Vegetation: There are 12 species of plants (5 trees, 1 shrub, 6 herbs), 44% of the atoll's flora. Shark has one introduction, *Cocos*, forming 3 clumps along the lagoon beach (1% of the islet's area). Shark's rings of vegetation approximate the islet's outline. Herb mats dot the fine sand lagoonward, while to seaward they emerge from coarse rubble. The *Tournefortia* (to 7 m tall) eventually gives way to a 12-m-high *Pisonia* forest studded with *Cordia* and *Pandanus*. Centrally this mixed forest is unnaturally open, suggesting possible past disturbance.

Birds: Four species of seabirds bred in 1988: great frigatebird (118 pairs), brown noddies (37 pairs), black noddies (125 pairs), and white tern (44 pairs). red-footed boobies were nesting in 1990. The notable colonies of great frigatebirds and black noddies are due in part to the extensive *Pisonia* forest, covering half of the islet.

29. SCARLET CRAB ISLET (0.46 ha) (Figs. 28,55)

This motu was named by the authors in honor of *Coenobita perlatus*, the scarlet, fist-sized hermit crab that is abundant both here and on the entire atoll.

Physiography: Scarlet Crab, sixth in the chain and only 40 m long by 125 m wide, is a young motu shaped like a closed pair of lips. It skirts the southern shore of Shark, separated from it by a channel 16 m wide. Because its eastern end points into the lagoon, there is no true lagoon beach. Together with the next three islets, Scarlet Crab's seaward reef flats (480 m) are the most extensive on Caroline's lee side.

Vegetation: Vegetative cover is slight: less than 1% area coverage of *Heliotropium* and *Laportea*, interspersed with 10 small *Tournefortia* (to 1.5 m). Its species count is 6 (1 shrub, 5 herbs), 22% of Caroline's flora. There are no introductions.

Birds: Although during storms this motu is undoubtedly awash, two species of seabirds were breeding in 1988: brown noddies (one pair, on ground) and white tern (two pairs, in low scrub).

30. MOTU NAUTONGA "Sea Cucumber Islet" (0.34 ha) (Figs. 28,55)

We named this motu for the Gilbertese word for the black sea cucumbers or "beche-de-mer" (*Ludwigothuria* sp.) that are densely strewn over all of Caroline's reef shallows (Pl. 10).

Physiography: Semicircular in shape, Nautonga is seventh in the Central Leeward chain, measuring 70 m long and 80 m wide. Situated close to the lagoon, it is one of three small islets that barely protrude above the reef flats. Nautonga's perimeter beaches are all narrow (2 m), and its seaward reef flats are wide (495 m).

Vegetation: There are nine indigenous species (three trees, one shrub, five herbs), 33% of the atoll's flora. Though small, Nautonga's vegetation is concentrically zoned, comprising herb mats (10–14 m wide), and a central forest of *Tournefortia* and *Pisonia* (84 m wide) up to 10 m high.

Birds: Five species of seabirds bred in 1988: red-footed booby (11 pairs), great frigatebird (2 pairs), brown noddly (7 pairs), black noddly (32 pairs), and white tern (10 pairs). Lesser frigatebirds appeared to be preparing to nest in May 1990. One pair of blue-gray noddies, flying toward Azure Isle, was seen by the 1990 expedition in May.

31. AZURE ISLE (0.20 ha) (Figs. 28,55; Pl. 53)

We named this small, wedge-shaped motu for the striking blue-green of its nearby lagoon.

Physiography: Eighth from the north, this small, elongated triangle of land is 30 m long and 66 m wide. Its seaward reef flats are wide (512 m). Its surge channels are narrow and shallow.

Vegetation: Azure has only seven species (one tree, one shrub, five herbs), 26% of Caroline's flora. The *Pisonia* tree is 6 m tall. A young motu, Azure is a superb example of an early stage of biological succession. Its plant cover consists of a single mound of *Tournefortia* scrub crowned by a single *Pisonia* tree, growing from rubble only one meter above sea level. Only 45% of its surface is vegetated; the rest, primarily on the ocean side, is coarse rubble. Azure Isle presents what may be the minimum width of vegetation (38 m) in which *Pisonia* can develop on Caroline.

Birds: This motu illustrates the speed at which seabirds will utilize newly available habitats. Within its dozen or so *Tournefortia* shrubs (to 4 m tall), three species of seabirds nest: red-footed booby (7 pairs), great frigatebird (2 pairs), and white tern (2 pairs). A pair of blue-gray noddies were seen in May 1990.

32. REEF-FLAT ISLET (0.09 ha) (Figs. 27,55)

We named this young motu for its primary characteristic—its reef flats. Ninth in the Central Leeward chain, this curved strip of coarse rubble lies parallel to the surge channels that surround it. It measures about 20 m long and 60 m wide. Only three species of plants are present (one shrub, two herbs), 11% of Caroline's flora. They cover less than one-fourth of its area and are distributed so sparsely that not one bird was present.

33. BIRD ISLET (4.05 ha) (Figs. 29,55)

This is one of the motus named on Arundel's chart (Fig. 4), probably reflecting the presence of black noddies and/or sooty terns.

Physiography: Bird is ovoid, measuring 230 m long by 200 m wide. It sits close to the inner edge of the lagoon reef, whereas 400 m of seaward reef flats stretch westward.

Vegetation: There are 12 species of plants (4 trees, 2 shrubs, 6 herbs), 44% of Caroline's flora. A small *Cocos* grove is the only introduction. It is well wooded, with very narrow herb mats (6% of total area). *Tournefortia* (to 8 m) and *Pisonia* (to 14 m) each cover 42% of its surface; the rest is rubble. The *Pisonia* forest is of good quality (90–95% canopy cover), having scattered *Morinda*, *Boerhavia*, and *Achyranthes*

as an understory. One large clump of *Suriana* (14 × 14 m, 2.5 m high) occurred in the islet center (A. Garnett, personal observation). Bird Islet shows very few signs of past disturbance, having prime plant communities, rich in breeding seabirds.

Birds: Five species of seabirds nested in 1988: red-footed booby (29 pairs), great frigatebird (6 pairs), brown noddly (42 pairs), black noddly (329 pairs), and white tern (48 pairs). In June 1990, many thousands of sooty terns laid on Bird and adjacent Fishball.

34. FISHBALL ISLET (0.57 ha) (Figs. 28,55,56)

Eleventh and southernmost in the Central Leeward chain, we named Fishball after discovering a large glass fishing float with a broken bottom, decorously placed in the islet's center within a square of coral slabs.

Physiography: *Paramecium*-shaped, Fishball lies close to the lagoon and is separated from Bird by a shallow, rubble-strewn channel 100 m wide. The motu is 45 m long by 144 m wide, with seaward reef flats 595 m in extent. South of the islet, the reef flats—wadable at very low tide—stretch 1.4 km to the Southern Leeward Islets.

Vegetation: The number of plant species is eight (one seedling "tree," one shrub, six herbs), 30% of Caroline's flora. Figure 56 depicts an east–west cross-section of Fishball, showing a vertical profile and the relative abundance and distribution of each species. Fishball exemplifies an emerging motu. All plants are low and halophytic; most are herbs. The motu is half-covered with a sparse herb mat of *Heliotropium* (10% cover), with scattered *Laportea*, *Lepturus*, and *Portulaca* (less than 1% cover each). Small *Tournefortia* shrubs (to 2 m tall) are scattered in the central sector, while a tiny drift seedling of *Morinda*, 7 cm high, struggled to gain a foothold in the exposed, salty rubble.

This motu is a fine example of the initial stages of islet formation and colonization. It demonstrates that sea-dispersed, halophytic herbs first germinate on the coarse rubble, later becoming shaded out by *Tournefortia*, enabling a greater plant species diversity to establish. It is very unlikely that a water lens is present.

Birds: Two species of seabirds bred in 1988: red-tailed tropicbird (three pairs) and brown noddly (five pairs). In May 1990, many thousands of sooty terns covered the ground and swirled in the air, day and night. On 23 May, no eggs were found, but laying occurred on Fishball and adjacent Bird Islet in June (A. Falconer, personal communication).

Southern Leeward Islets (Pls. 14, 78)

This chain of five small motus lies along the southwestern edge of the lagoon. All are built upon piles of rubble about 3 m high, oriented in an east–west direction, and are separated by shallow, narrow channels. They range in size from 1.51 to 3.67 ha, and their topography, vegetation, and breeding seabirds are similar. Although situated on the leeward side of the atoll, the Southern Leeward Islets exhibit some windward characteristics: they lie opposite and slightly north of a wide break in the windward reef, which allows trade winds to sweep,

uninterrupted, across the lagoon. This promotes their 60–80% cover of scrub or forest. Ana-Ana, the southernmost, was periodically occupied from 1987–1991 by the Falconer family.

Of particular botanical interest are the interior forests, composed of *Pisonia* mixed with more *Cordia* than elsewhere on the atoll. Pure *Cordia* groves (mostly too small to map accurately) typically occupy the forest periphery.

Their history (apart from the last 3 years) is unknown; all appear to harbor virgin plant communities with occasional drift-derived *Cocos* or *Pandanus*.

35. MOTU RAURAU “Blue-gray Noddy Islet” (3.48 ha) (Figs. 29,57; Pls. 14,78,79)

Northernmost of the Southern Leeward Islets, we named this motu for the blue-gray noddies (*raurau* in Gilbertese) observed there. A highly territorial blue-gray noddy was acting as though a nest was nearby.

Physiography: Raurau is ovoid, with a small lagoonside bay, and maximum dimensions of 180 m long and 231 m wide. It has the most expansive rubble of all the Southern Leeward Islets. This coarse coral clinker extends, apronlike, around the islet, widest (40 m) closest to the lagoon and narrowest (10 m) to seaward. The seaward reef flats extend 446 m to the ocean.

Vegetation: The number of plant species is 10 (5 trees, 1 shrub, 4 herbs), 37% of the atoll’s flora. Raurau’s two plant communities are simple: a very scant herb mat is sprinkled with *Tournefortia*, which rises to 6-m-high scrub all around the islet. *Laportea* forms a narrow band at the interface between coral rubble and scrub. Centrally a *Pisonia* forest (to 13 m), dotted with *Cordia* on the periphery, harbors much *Morinda* in the understory, including the tallest *Morinda* (13 m) seen on the atoll. A handful of drift-derived *Cocos* and *Pandanus*, the only introductions, dot the scrub.

Birds: No seabirds were found on transect, but a perimeter walk in 1988 revealed that four species bred on the west side in the *Tournefortia* scrub: red-footed booby (10 pairs), great frigatebird (31 pairs), brown noddy (1 pair), and white tern (2 pairs). This islet, for its size, is particularly rich in frigatebirds.

Comments: Polynesian rats are present.

36. MOTU EITEI “Frigatebird Islet” (1.41 ha) (Figs. 29,57; Pls. 14,78)

Second in line from the north, we named this motu for its nesting great frigatebirds, *eitei* in Gilbertese.

Physiography: Motu Eitei is fat-elliptical, 105 m long and 280 m wide. Lying perpendicular to the reef axis, it touches the lagoon edge on its inner side. To seaward, the reef flats are 644 m wide.

Vegetation: There are eight species of plants (three trees, one shrub, four herbs), 30% of the atoll’s flora, with no introductions. Eitei is carpeted with three plant communities in the usual concentric arrangement. However, there is a slight difference in the species composition of the herb mats: on transect, the southern mat (2 m wide) consisted solely of *Portulaca*, while the north side contained a 3-m swath of *Heliotropium*, *Laportea*, and scattered *Suriana*. Inside the mat

is a ring of *Tournefortia* scrub (to 5 m) and a central *Pisonia*–*Cordia* forest (to 11 m). *Laportea* is particularly abundant, while *Portulaca*, normally confined to the edges, abounds in small openings within the interior woodlands.

Birds: Four species of seabirds bred on Motu Eitei in 1988: red-footed booby (17 pairs), great frigatebird (14 pairs), brown noddy (6 pairs), and white tern (18 pairs). The first blue-gray noddy nest for Caroline was found in summer, 1990 (Subchapter 1.2, this volume).

37. PISONIA ISLET (2.45 ha) (Figs. 29,57; Pls. 14,78)

We named this motu for its fine *Pisonia* forest.

Physiography: *Pisonia*, third in the chain from the north, is almost circular and lies closely appressed to its neighbor islets. Its maximum dimensions are 140 m long and 220 m wide. Like Raurau, it possesses a wide “apron” of coral rubble and sparse herbs on the lagoon side. Its seaward reef flats are 300 m wide.

Vegetation: The number of plant species is 15 (5 trees, 2 shrubs, 8 herbs), 56% of the atoll’s flora. The only introduction is *Cocos* (few, scattered, north and south shores). Well wooded, *Pisonia* harbors the customary three plant communities: the herb mat is almost pure *Heliotropium*, dotted with *Suriana*. One specimen of *Lepidium bidentatum* was found in 1990. The *Tournefortia* scrub and forest, covering half of the motu’s length and width, grows to 9 m, while the *Pisonia*–*Cordia* forest, covering 0.86 ha (35% of the islet’s area), reached 10 m.

Birds: Despite the beautiful *Pisonia* forest, no black or brown noddies nested. Only three species of seabirds bred in 1988: red-footed booby (26 pairs), great frigatebird (14 pairs), and white tern (10 pairs). Best represented were red-footed boobies; a perimeter count yielded 18 tended nests, all in *Tournefortia* scrub. A long-tailed cuckoo was heard in the interior.

Comments: Rats were common: six were noted on a mid-morning transect survey.

38. MOTU KIMO A “Rat Islet” (1.80 ha) (Figs. 29,57; Pls. 14,78,80)

Fourth from the north, we named this motu for its single mammalian inhabitant, the Polynesian rat, *kimoa* in Gilbertese.

Physiography: Kimoa, smallest of the Southern Leeward Islets and shaped like a flared teardrop, is squeezed between its neighbor motus. Its maximum dimensions are 92 m long and 218 m wide, almost four times the size mapped by Arundel (Fig. 4). The southeast rubble and herb mats are wide. The distance to the outer reef edge is 307 m. Of special note is the emergent *Tridacna*–*Acropora* reef, which stretches completely across the lagoon to Tridacna Islet. This reef is 15–20 m wide (Fig. 48; Pls. 26, 63) and 1,023 m long, which, together with an equal length in blind diverticulae, totals over 2 km. The *Tridacna* clams aggregate in densities up to 80/m² (Sirenko & Koltun, Subchapter 1.4).

Vegetation: Kimoa has 11 species of plants (3 trees, 2 shrubs, 6 herbs), 41% of Caroline’s flora. There are no introductions. Though small and narrow, Kimoa is well

vegetated. Its herb mats are composed of *Heliotropium* on the south side and *Portulaca* (plus *Suriana*) on the north. The interior *Tournefortia*–*Pisonia*–*Cordia* forests (to 11 m) cover nearly one-half of the islet's area.

Birds: Four species of seabirds bred in 1988: red-footed booby (21 pairs), great frigatebird (3 pairs), black noddy (2 pairs), and white tern (7 pairs). Red-footed booby nests were located along the perimeter.

39. MOTU ANA-ANA "Anne's Islet" (2.16 ha) (Figs. 29,57; Pls. 5a,14,54,78,81)

This motu includes a small settlement with three thatched huts (cooking, eating, sleeping), a water tank, chicken coop, and garden. It was occupied from 1989–1991 by Anne and Ron Falconer, 2 small children, chickens, Muscovy ducks, and a dog. When we discovered a wooden sign marked "Ana-Ana" and adorned with a shell lei, we knew the islet had been named.

It is interesting to compare Pls. 5a and 81, identical views of Ana-Ana 105 years apart. The profiles are indistinguishable, showing how little this motu has changed over the years.

Physiography: Ana-Ana is the southernmost motu in the Southern Leeward Islets, 120 m long by 222 m wide at its widest point. Approximately 3 m high, it is roughly oval, with a hooked point and curved bay facing the lagoon. This point is actively growing as more and more rubble is deposited by the large flow of water passing through the channel (430 m wide) that separates Ana-Ana and South Island. This channel contains abundant giant clams that amass into an extensive *Acropora*–*Tridacna* reef stretching approximately 900 m across the lagoon to Tridacna Islet. The outer reef flats measured 281 m.

Vegetation: Ana-Ana has 15 species of plants (5 trees, 2 shrubs, 8 herbs), 56% of Caroline's flora. Introductions include *Cocos*, vegetables, a few ornamentals and, as yet, no weeds. Ana-Ana's vegetation is typical of the other Southern Leeward Islets, except for the settlement. Narrow trails from the southern channel lead to a neat clearing, approximately 40 m × 70 m, the only inhabited portion of the atoll. We have advised the Falconers against introducing exotic plants with spreading seeds and have requested them to destroy all introductions when vacating the island permanently.

Ana-Ana has sparse strand vegetation: *Suriana*, *Heliotropium*, *Portulaca*, *Laportea*, and *Lepturus*. The *Tournefortia* scrub includes *Cocos*, *Cordia*, and *Pandanus*. A quality *Pisonia* forest, 15 m high, covers 43% of the islet's area.

Birds: No breeding seabirds were found on any of the three visits to Caroline. However, the Falconers have found a few white terns and one great frigatebird nesting in the perimeter scrub, as well as groups of brown noddies sitting on the beach. Long-tailed cuckoos were seen around the huts in March, April, and May 1990.

Comments: Rats are abundant. Although the house site was clean and tidy, 12 rats were seen in a pile of coconut debris, and others scurried amongst the forest litter. The Falconers

have trapped over 1,300 rats in less than 2 years. Several pale geckos with a few spots and largish heads were seen in and around the thatched huts (probably mourning geckos).

Conclusion

Lushly wooded Caroline Atoll, with the majority of its 39 islets (399 ha of land) either in near-pristine condition or having recovered remarkably from past disturbance, is one of the least spoiled atolls in the Pacific. Uninhabited except for one family, it harbors plant ecosystems and breeding seabirds (Subchapter 1.2, this volume) of national and international importance. Its marine and terrestrial ecosystems are prime outdoor ecological laboratories for research on geological processes including groundwater, fish poisoning, and numerous facets of ecology (especially plant succession). Caroline boasts outstanding coral reefs thickly studded with giant clams, substantial numbers of coconut crabs, breeding sites for green turtles, wintering grounds for shorebirds including the rare bristle-thighed curlew, ancient Tuamotuan *marae*, and a crystalline lagoon. The variety, abundance, and quality of its flora and fauna qualify it for status as an officially recognized international preserve (Subchapter 1.2, Conservation section).

An expedition of this magnitude entailed the help of many people, and it gives us great pleasure to thank them. We are indebted to Hal O'Connor and Randy Perry, Patuxent Wildlife Research Center, for making possible our participation. Steve Kohl, FWS Office of International Affairs, and Terry Whitledge aided immensely by handling innumerable details with their Soviet colleagues. Members of the Fish & Wildlife Service Mauna Loa Field Station, especially Jim Jacobi, Julia Williams, Jack Jeffrey, and Martha Moore, provided welcome logistical support in Hilo, and Paul Sykes willingly shouldered additional responsibility that freed CBK to join the expedition.

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skipper/owner of *Te Manu*, who transported us 7,400 km in the central Pacific (including two visits to Caroline), helped with field work, and whose competence and consideration in many areas eased the varied hardships associated with 3 months at sea in a 10.5-m ketch. Thanks also to Scott Miller for providing insect vials and for preparing and depositing insect specimens in the Bishop Museum, Hawaii.

On remote Caroline, the Falconers were exceptionally hospitable hosts, developing a special interest in its wildlife and helping us with field work during and after the expedition. Special thanks go to 7-year-old Alexandre, who discovered the first blue-gray noddy nest for the island and 3 new plant records.

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TABLE 1

Plants reported from Caroline Atoll, but considered to be transient or extinct members of the flora.¹

Scientific Name	English and Gilbertese Names	Date Last Reported	Comments
CLASS ANGIOSPERMAE			
Family Graminae			
<i>Eleusine indica</i> (L.) Gaertn.	goosegrass, <i>te uteute</i>	1884	Introduced weed
<i>Eragrostis amabilis</i> (L.) H. & A.	lovegrass, <i>te uteute</i>	1884	Introduced weed
Family Cyperaceae			
° <i>Kyllinga brevifolia</i> Rottb.	kyllinga		One clump by cistern, South Is., on recently disturbed ground
Family Bromeliaceae			
<i>Ananas comosa</i> L.	pineapple, <i>te bainaboro</i>	1884	Introduced for cultivated fruit
Family Liliaceae			
<i>Crinum</i> sp.	lily, <i>te kiebu</i>	1884 Presently cultivated	Introduced ornamental. One small specimen found on South Is. by Anne Falconer, 1990. Collection no. K-90-14
Family Moraceae			
° <i>Artocarpus altilis</i> (Park.) Fosb.	breadfruit, <i>te mai</i>	Presently cultivated	Not yet established, 2 trees on South and Ana-Ana
<i>Ficus carica</i> L.	common fig, <i>te biku</i>	1884	Introduced for cultivated fruit
Family Basellaceae			
<i>Boussingaultia gracilis</i> Miers	Madeira vine	1884	Introduced "vine climbing over portico" (Trelease 1884)
Family Leguminosae			
<i>Inocarpus fagifer</i> (Parkins. ex Z) Fosb. (= <i>I. fagiferus</i>)	Tahitian or Pacific chestnut, <i>mape</i> (Tahiti), <i>te ibi</i>	1840	Unsuccessful introduction in 1834. Food plant
Family Euphorbiaceae			
<i>Euphorbia hirta</i> (= <i>E. pilulifera</i>)	garden spurge, sleeping plant, <i>te kaimatu</i>	1884	Introduced weed, unsuccessful
Family Guttiferaceae			
<i>Calophyllum inophyllum</i> L.	Alexandrian laurel, <i>tamanu</i> (Tahiti), <i>te itai</i>	1884	In the 1940's, a "few taller <i>Calophyllum</i> and <i>Pisonia</i> " (N.I.D. 1943). No other reference; did observer confuse <i>Calophyllum</i> with <i>Cordia</i> ?
Family Caricaceae			
<i>Carica papaya</i>	Papaya, pawpaw, <i>te babaia</i> , <i>te mwemwera</i>	Presently cultivated	Cultivated for fruit in 1884, not seen in 1965. In garden on Ana-Ana, one on South Is. by cistern
Family Cucurbitaceae			
<i>Cucurbita pepo</i> L.	Pumpkin, <i>te baukin</i> , <i>te bamakin</i>	Presently cultivated	Cultivated in 1884, not found in 1965
<i>Ipomoea batatas</i> L.	Sweet potato, <i>te kumara</i>	Presently cultivated	Introduced in 1840, not reported again until this expedition (tubers brought in 1988). Collection nos. K-159, 160
<i>Ipomoea caprae brasiliensis</i> (L.) v. Ooststr.	beach morning glory, <i>pohuehue</i> (Hawaii), <i>te ruku</i>		Found in 1965 by copra shed; extensive searching on 3 expeditions in 1988 and 1990 failed to find it
Family Scrophulariaceae			
<i>Russelia equisetiformis</i> Schlecht.	Coral plant, <i>te kaibaun</i> ("golden plant")	1884	Unsuccessful introduction in 19th century

¹Since 1988, the Falconers have added more vegetables and ornamentals to their ever-expanding garden: green beans, lemon grass, peppermint, okra, banana, Tahitian gardenia (*tiare*), tomato, breadfruit, red hibiscus, etc.

°Not previously reported from Caroline Atoll.

TABLE 2

Vascular flora of Caroline Atoll: relative abundance of each species within the major ecosystems, with data on seabird utilization¹

Scientific Name	Common & Gilbertese Name	Seabird Utilization		Natural Ecosystems					Anthropogenic Ecosystems		
		Breeding	Roosting	Coastal		Inland			Coconut Woodlands		
				Natural	Beach	Tourn.	Tourn.	Pisonia	Cocos	Dying	Mixed
				Herb Mat	Scrub With <i>Suriana</i>	Scrub	Forest	Forest	Plantation	<i>Cocos</i> Plantation	Forest With <i>Ipomoea</i> Cocos
TREES											
<i>Pisonia grandis</i>	pisonia, puka tree, <i>te buka</i>	X	X		R	UC	C	A	L,UC	L,UC	R-C
<i>Morinda citrifolia</i>	Indian mulberry, <i>te non</i>			D	C	R-C	R-VC	R-A	R-C	C	O
<i>Cocos nucifera</i>	coconut, <i>te ni</i>	X	X			R-O	UC	O	A	A	C-A
<i>Cordia subcordata</i>	sea trumpet, kou (Hawaii), <i>te kanawa</i>	X	X			UC	UC-C	R-VC		L,UC	R
<i>Pandanus tectorius</i>	pandanus, screwpine, <i>te aroka, te kaina</i>	X	X		O	C	C	O	O		A
<i>Hibiscus tiliaceus</i>	beach hibiscus, <i>hau</i> (Hawaii), <i>te rau</i>								L,R		
<i>Thespesia populnea</i>	<i>milo</i> (Hawaii), <i>te bingibing</i>								L,R		
SHRUBS											
<i>Tournefortia argentea</i>	tree heliotrope, <i>te ren</i>	X	X	O-UC	VC	A	A	UC-A	UC		C
<i>Suriana maritima</i>	bay cedar, <i>te aroa, te marou</i>			O	VC-A	O					
<i>Ximenia americana</i>	monkeyplum								LA		
<i>Scaevola sericea</i>	scaevola, saltbush, half-flower, <i>te mao</i>			R		S					
Species A											
HERBS											
<i>Heliotropium anomalum</i>	"sand rose", <i>hinahina</i> (Hawaii)	X	X	A	UC	VC					
<i>Boerhavia repens</i>	pigvine, <i>te wao</i>			R-UC	R-C	R-A	R-A	R-A	UC-A	UC	C-A
<i>Portulaca lutea</i>	yellow portulaca, seaside purslane, <i>te bointari, te boi</i>			O-A	R-UC	UC-C	O	L,O		R-C	R
<i>Laportea ruderalis</i>	"nettle", <i>te ukeuke, te nekeneke</i>			R-VC	UC	C-A	C	LC	LC	R-UC	UC-C
<i>Achyranthes canescens</i>						R-C	C	C	O		A
<i>Phymatosorus scolopendria</i>	maile-scented fern, <i>laua'e</i> or lawai fern, <i>te rankota, te keang</i>				R	LC	LC	C-A,L	R-A	R-UC	C-A
<i>Lepturus repens</i>	bunchgrass, <i>te uteute</i>			R-UC	UC-A	L,R-A			R		
<i>Ipomoea macrantha</i>	morning glory, wild moon-flower, <i>te ruku</i>					R	R	R-UC	UC	A	
<i>Tacca leontopetaloides</i>	Polynesian or island arrowroot, <i>pia</i> (Hawaii & Tahiti), <i>te makemake</i>								LA		
<i>Lepidium bidentatum</i>	peppergrass			L,R		LR					
<i>Psilotum nudum</i>	upright psilotum, "reed fern", <i>te kumarawa</i>								LR		
<i>Phyllanthus amarus</i>									LR		
<i>Sida fallax</i>	<i>'ilma</i> (Hawaii), <i>te kaura</i>								LR		
+ <i>Digitaria</i> sp.	crabgrass, <i>te uteute</i>								(S)		
<i>Tribulus cistoides</i>	puncture vine, <i>te kiebu</i>			R							

¹ Excludes transient and extinct species (Table 1). Species arranged according to their overall abundance on the atoll.

* New records for Caroline.

Not seen on this expedition, last seen 1965 (Clapp & Sibley, 1971a).

TABLE 3

Distribution and abundance of plant species on Caroline Atoll.¹ Motus are arranged geographically from north to south (windward), then similarly on the leeward side.

		Windward Motus														South Nake Motus							
N	L	B	W	C	A	N	P	S	N	B	N	N	A	T	S	P	D	B	C	L	K	M	
a	o	o	i	r	t	o	i	k	o	r	o	o	r	r	o	a	a	o	o	o	o	o	
k	n	'	n	e	i	r	g	u	r	o	d	r	u	i	u	n	n	o	r	n	t	u	
e	g	s	d	s	h	t		l	t	t	d	t	n	d	t	d	g	b	a	e	a	a	
		u	w	c	u	h		l	h	h	y	h	d	a	h	a	e	y	l			k	
		n	a	e						e			e	c		n	r			P	e	n	
		r	n			P			B	r	R	A	l	n		u				a			
		B	d	t		i			r	s	o	r		a		s				l		a	
		i				g			o		c	u							m				
		r							t		k	n											
		d							h			d											
									e			e											
									r			l											
									s														
<hr/>																							
TREES (7 spp.)																							
<i>Pisonia grandis</i>	A	VC		A	A		A	A		A	A		VC	A	R	R	VC	A	VC	UC	R	R	R
<i>Morinda citrifolia</i>	UC	UC		UC	O		R	UC		R	O		O	UC	VC	C	R	R	R	R	R	R	
<i>Cocos nucifera</i>	LA	LA						LR			LO		R			A				LR	LR		
<i>Cordia subcordata</i>	UC	UC		C	LA		C	VC		C	VC		C	UC		R		LA					
<i>Pandanus tectorius</i>	LA															LO	LA						
° <i>Hibiscus tiliaceus</i>																LR							
° <i>Thespesia populnea</i>																LR							
<hr/>																							
SHRUBS (5 spp.)																							
<i>Tournefortia argentea</i>	A	A	VC	A	A	O	A	A	O	A	A	O	A	A	A	C	A	A	A	A	A	C	A
<i>Suriana maritima</i>		LR									LR				LC	UC, LC							
° <i>Scaevola sericea</i>				S																			
° <i>Ximenesia americana</i>																LA							
°Species A																							
<hr/>																							
HERBS (15 spp.)																							
<i>Heliotropium anomalum</i>	C	VC	UC	C	C	UC	UC	UC	R	UC	C		O	UC	VC	C	C	O	UC	UC	UC	UC	R
<i>Boerhavia repens</i>	C	LC		C	C		C	C		UC	C		A	UC	C	VC	C	O	O	R	R	R	R
<i>Portulaca lutea</i>	C	C	C	C	C	UC	UC	C	C	A	A	A	A	C	C	C	C	UC	O	O	O	O	R
<i>Laportea ruderalis</i>	C	VC		C	UC		UC				C			C	UC	UC	C	O	O	R	R	R	R
° <i>Achyranthes canescens</i>	LC	O			O		C	O		LC			VC	VC	LC	R	O	O	R	R	R	R	R
<i>Lepturus repens</i>	R	R	R	R			R			R	R	C		C	C	O	R	R	R	R	R	R	R
<i>Phymatosorus scolopendria</i>	VC	LA, UC			UC		UC	UC						O	C	LA, UC				R	R		
<i>Ipomoea macrantha</i>	LC	O		UC				O								A							
<i>Tacca leontopetaloides</i>	*LC															LR							
<i>Psiloton nudum</i>	*LR															LR							
<i>Phyllanthus amarus</i>																LC							
<i>Tribulus cistoides</i>		S																					
<i>Sida fallax</i>																LR							
<i>Lepidium bidentatum</i>																S							
* <i>Digitaria</i> sp.																S							

TABLE 3 - continued

	Central Leeward Motus											Southern Leeward Motus					T	% O	O
	M	B	M	E	S	S	N	A	R	B	F	R	E	P	K	A			
	a	l	a	m	h	c	a	z	e	i	i	a	i	i	i	n	o	n	r
	n	a	t	e	a	a	u	u	e	r	s	u	t	s	m	a	t	F	i
	n	c	a	r	r	r	t	r	-	d	h	r	e	o	o	-	a	r	E
	i	k	w	a	k	l	o	e	f		b	a	i	n	a	A	l	e	a
	k	f	a	l		e	n		f		a	u		i		n	q	c	
	i	i		d		t	g		l		l			a		a	u	h	
	b	n					a		a		l						e		
	a					C			t								n	M	
						r											c	o	
						a											y	t	
						b											u ²		
TREES (7 spp.)																			
<i>Pisonia grandis</i>	C	VC	UC	C	A		O	R		A		A	C	A	VC	A	32	82	1
<i>Morinda citrifolia</i>	R		R	R	R		R			R	D	UC	R	R	R	C	30	77	1, AI?
<i>Cocos nucifera</i>	LR	LR		LO	LR					LR		LR		LO		LC	17	44	AI, RI
<i>Cordia subcordata</i>	O	UC	C	O	LO		O			UC		C	C	C	C	C	23	59	1
<i>Pandanus tectorius</i>			R	C	C							LR		LR		LR	9	23	1, AI?
^o <i>Hibiscus tiliaceus</i>																	1	3	1 (AI, RI?)
^o <i>Thespesia populnea</i>																	1	3	1 (AI, RI?)
SHRUBS (5 spp.)																			
<i>Tournefortia argentea</i>	A	A	A	A	A	R	C	C	R	A	UC	A	A	A	A	A	39	100	1
<i>Suriana maritima</i>			R							UC			LR	LR	LR	O	10	19	1
^o <i>Scaevola sericea</i>																	1	3	1
^o <i>Ximenesia americana</i>																	1	3	
^o Species A	S																1	3	1
HERBS (15 spp.)																			
<i>Heliotropium anomalum</i>	C	C	C	C	C	R	C	C	R	R	UC	UC	C	C	C	UC	38	98	1
<i>Boerhavia repens</i>	C	UC	UC	C	UC	R	R	R		UC	R	UC	UC	UC	O	C	34	88	1
<i>Portulaca lutea</i>	C			C	UC	R	R	R	R	UC	R	UC	C	UC	C	LC	37	95	1
<i>Laportea ruderalis</i>	UC	UC	O	C	UC	R	R	R		R	R	UC	VC	UC	O	C	32	82	1
^o <i>Achyranthes canescens</i>	UC	O	R	UC	LA		R	R		UC	R			O	C	O	29	72	1
<i>Lepturus repens</i>	R	R		R		R				UC	R			R	R	UC	27	69	1
<i>Phymatosorus scolopendria</i>	O				R											UC	14	36	1
<i>Ipomoea macrantha</i>														O		R	7	18	1
<i>Facca leontopetaloides</i>																	1	3	RI, AI?
<i>Psilotum nudum</i>																	1	3	1
<i>Phyllanthus amarus</i>																	1	3	X
<i>Tribulus cistoides</i>																	1	3	1
<i>Sida fallax</i>																	1	3	1
<i>Lepidium bidentatum</i>														S			2	5	1
^o <i>Digitaria</i> sp.																	1	3	?

^o Species arranged according to frequency of occurrence. List excludes transient and extinct members of the flora (Table 1).

¹ No. motus having a particular species, divided by total no. motus x 100%.

² New records for Caroline.

Not seen on three visits, but possibly still present.

TABLE 4

Sizes of Pacific atoll floras, with emphasis on the percentages of indigenous plants.¹

Island Group	Atoll	Total ² No. Species	No. Species Indigenous	% Indigenous	Source
Caroline Is. (Fed. States of Micronesia)	Kapingamarangi	98	38	39	Niering, 1962
Cook Is. (New Zealand)	Aitutaki (motus)	45		50	Stoddart & Gibbs, 1975
	Rarotonga (motus)	49		ca. 60	Stoddart & Fosberg, 1972
Gilbert Is. (Rep. of Kiribati)	Onotoa	60	50	83	Moul, 1957
	Tarawa	109	28	26	Catala, 1957
Northwest Hawaiian Is. (USA)	Kure	42	23	55	Lamoureux, 1961; Clay, 1961
	Laysan	38	27	71	Ely & Clapp, 1973
Line Is. (Kiribati)	Caroline	27	23(25?)	85(93?)	This paper
	Christmas (Kiritimati)	69	19	28	Garnett, 1983
	Fanning	123	23	19	Wester, 1985
	Flint	37	14	38	St. John & Fosberg, 1937
	Malden	9	9	100	Garnett, 1983
	Palmyra	58	21	36	Wester, 1985
	Starbuck	7	4	57	Garnett, 1983 (incomplete, little known)
	Vostok	3	3	100	Clapp & Sibley, 1971b; Kepler, 1990c
Marshall Is. (Fed. States of Micronesia)	Washington	91	25	27	Wester, 1985
	Ailuk	56	26	46	Fosberg, 1955
	Arno	125	40	32	Hatheway, 1953
	Enewetak	128	55	43	Lamberson, 1987
	Jaluit	288	55	21	Fosberg & Sachet, n.d.
	Jemo	34	17	50	Fosberg, 1955
	Kwajalein	89	25	28	Fosberg, 1955, 1959
	Lae	61	35	57	"
	Likiep	91	31	34	"
	Taka	23	18	78	Fosberg, 1955
	Ujac	61	32	52	Fosberg, 1955, 1959
	Ujelang	50	29	58	"
	Utirik	55	26	47	"
	Wotho	40	28	70	"
Phoenix Is. (Kiribati)	Kanton (Abariringa)	164	14	9	Degener & Gillaspy, 1955
		129	18	14	Garnett, 1983
	Birnie	3	3	100	Fosberg & Sachet, (n.d.)
	Enderbury	23	18	78	"
	Nikumaroro	35	17	49	"
	Orona	ca. 29	19	ca. 66	"
	McKean	7	7	100	"
	Phoenix	6	6	100	"
	Manra	ca. 18	14	ca. 77	"

TABLE 4 - *continued*

Island Group	Atoll	Total ² No. Species	No. Species Indigenous	% Indigenous	Source
Society Is.	Tetiaroa	95	47	49	Sachet & Fosberg, 1983
Solomon Is.	Ontong Java	150	58	39	Bayliss-Smith, 1973
Tokelau Is. (N.Z.)	Nukunono	55	35	64	Parham, 1971
Tuamotu Is. (France)	Rarioa	121	39	32	Stoddart & Sachet, 1969
	Rarioa	135	54	40	Doty, 1954
	Takapoto	106	33	31	Sachet, 1983
Outlyers	Clipperton (U.K.)	31	14	45	Sachet, 1962
	Oeno (U.K.)	17	14	82	St. John & Philipson, 1960
	Wake	94	20	21	Fosberg & Sachet, 1969

¹An updated version of Table 11, p. 105, Stoddart and Gibbs (1975).

²Number of species of those indigenous are not always comparable. Ferns are usually included, but certain ornamentals may not be. *Artocarpus*, *Morinda*, and *Pandanus* may be indigenous, aboriginal introductions, or both. Without its full scientific name, a species has an unknown biogeographical status.

TABLE 5

The distribution of plant subcommunities, together with the number of plant species on the motus of Caroline Atoll. Motus are arranged according to increasing area, illustrating seral stages in plant succession.

Motu	Area Category/ ha	Motu Area/ ha	Number of Plant Species ¹				Natural Plant Subcommunities					Anthropogenic Plant Subcommunities					
			Trees	Shrubs	Herbs	Total	Coastal			Inland		Cocos Plantation	Dying Cocos/ Ipomoea Forest	Mixed Forest With Cocos			
							Natural Herb Mat	Beach Scrub With Suriana	Pandanus Forest	Tournefortia Forest <5 m tall	Tournefortia Forest >5 m tall				Cordia Forest	Tournefortia/ Pisonia Forest	Pisonia Forest
<0.2																	
Noddy Rock		0.02	0	1	2	3	X										
Skull Islet		0.02	0	1	2	3	X										
Motu Atibu		0.02	0	1	2	3	X										
Reef-flat Islet		0.09	0	1	2	3	X										
0.2 - 0.7																	
Azure Isle		0.20	1	1	5	7	X				X						
Motu Nautonga		0.34	3	1	5	9	X				X						
Scarlet Crab		0.46	0	1	5	6	X				X						
Fishball Islet		0.57	1	1	6	8	X				X						
Motu Kota		0.64	3	1	7	11	X				X						
0.8 - 25.0																	
Booby Islet		0.84	2	1	6	9	X				X		X				
Bo'sun Bird Islet		0.86	0	1	3	4	X				X		X		X		
North Arundel Islet			0.91	4	1	6	11	X			X		X				
Motu Mouakena		1.00	1	1	6	8	X				X		X				
Motu Eilei		1.41	3	1	5	9	X		X		X		X				
Coral Islet		1.70	2	1	6	9	X				X		X				
Motu Matawa		1.71	4	2	4	10	X				X		X		X		
North Brothers Islet			1.71	3	1	5	10	X			X		X		X		
Motu Kimoa		1.80	3	2	6	11	X				X		X				
Lone Palm Islet		1.99	3	1	7	11	X				X		X				
Motu Ana-Ana		2.16	5	2	8	15	X		X		X		X				
Pisonia Islet		2.45	5	2	8	15	X		X		X		X				
Blackfin Islet		2.62	3	1	5	9	X				X		X				
Danger Islet		2.71	2	1	7	10	X				X		X				
Crescent Islet		3.10	3	1	6	10	X				X		X				
Motu Raurau		3.48	5	1	4	10	X		X		X		X				
Bird Islet		4.05	4	2	6	12	X				X		X				
Brothers Islet		4.31	3	2	5	10	X				X		X				
North Pig Islet		5.44	3	1	7	11	X				X		X				
Pandanus Islet		7.20	3	1	6	10	X				X		X				
Pig Islet		7.25	4	1	6	11	X				X		X				
Arundel Islet		7.34	3	1	7	11	X				X		X				
Shark Islet		7.98	5	1	6	12	X				X		X				
Emerald Isle		8.34	5	1	6	12	X				X		X				
Tridacna Islet		9.08	2	2	9	13	X				X		X				
Windward Islet		11.42	3	1	7	11	X				X		X				
Motu Marnikiba		21.49	4	2	7	13	X				X		X				
> 25.0																	
Long Island		75.98	4	2	9	15	X	X		X	X	f	c	e	l	X	
South Island		104.41	7	3	13	23	X	X	X		X	X	X	X	X	X	X
Nake Island		107.46	5	1	10	16	X	X	X		X	X	X	X	X	X	X

¹ Excludes transient and extinct species.

TABLE 6

Distribution and abundance of plant species in relation to motu size. Species are arranged according to their dispersal mechanisms: sea, bird, wind, man (aboriginal and "recent"). Within these categories, species are further subdivided in order of decreasing frequency on the motus.

	Size of Motu (ha)																						
	< 0.2											0.2 - 0.7											
	0.8 - 25.0											> 25.0											
	0.02	0.09	0.2	0.3	0.4	0.5	0.6	0.8	0.9	1.0	1.1-	2.1-	3.1-	4.1-	5.1-	7.0-	8.1-	9.1-	11.0-	21.0-	75.0-	104.0-	107.0-
(3)*	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(2)	(1)	(1)	(6)	(4)	(2)	(2)	(1)	(4)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
INDIGENOUS SPECIES																							
SEA-DISPERSED																							
<i>Tournefortia argentea</i>	R-O	C	C	C	R	UC	C	VC-A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A
<i>Heliotropium anomalum</i>	R	R	C	C	R	UC	UC	UC	R	R	O-C	R-C	UC	R-C	UC	UC-C	C	C	C	C	VC	C	C
<i>Portulaca laevis</i>	UC-A	R	R	R	R	R	O	O-C	C	R	R-UC	O-UC	C	A	UC	UC-C	C	C	C	C	VC	C	C
<i>Laportea radialis</i>		R	R	R	R	R	R	O	UC	R	R-VC	O-UC	UC	R-C	UC	UC-C	C	C	C	UC	VC	UC	C
<i>Achyroanthus canescens</i>		R	R	R	R	R	R	R	UC	R	R-C	O		UC	C	O-LA	UC	LC	O	UC	O	R	LC
<i>Lepurus repens</i>	R-C					R	R	R	R	R	R	R	R	R	R	R-C	R	C	R	R	R	O	R
<i>Cordia subcordata</i>				R-O					R		O-C	UC-LA	LA	VC	UC	UC	O	C	C	O	UC	R	UC
<i>Suriana maritima</i>											RL	O		O							LR	LC	LC
<i>Pandanus tectorius</i> ²											LR	LR				LR-LC	C		O		O	A	LC
<i>Iponoea macroantha</i>											LR-O					O				R,S			
<i>Scaevola sericea</i>																R-UC	R	VC	UC	R	UC	C	UC
<i>Morinda citrifolia</i> ²				R	D	R	R	R	R	R	R	R-UC	UC-O	R-O	R	R-UC	R					LR	
<i>Hibiscus tiliaceus</i> ³																							
<i>Theopestia populnea</i> ³																							
<i>Sida fallax</i>																							
<i>Lepidium bidentatum</i> ⁴																							
Species A*											S						S			R,S			LA
<i>Ximenesia americana</i> ⁴																							
*Digitaria sp.																							
BIRD DISPERSED																							
<i>Borreria repens</i>			R	R	R	R	R	O	O	R-UC	O-UC	UC-C	UC-C	UC-C	C	UC-C	C	C	C	C	LC	VC	C
<i>Pisonia grandis</i>	R	O	R	R	R	R	R	VC	VC	R-A	VC-A	A	A	A	A	VC-A	C	R	A	C	VC	R	A
<i>Tribulus cistoides</i>																					LR		
WIND-DISPERSED																							
<i>Phymatosorus scolopendria</i>							R	R	R			UC				R-UC		C		O	LA	LA	VC
<i>Psidium nudum</i>																					LA		*LR
INTRODUCED SPECIES																							
MAN-DISPERSED																							
Aboriginal Introductions																							
<i>Coccoloba nucifera</i>																							
"Recent" Introductions																							
<i>Tacca leontopetaloides</i>																							
<i>Phyllanthus amarus</i>																							

List includes transient and extinct members of the flora (Table 1).

"Recent" covers the time period 1834 to an unknown date in the 20th century.

Possibly also an aboriginal introduction.

Dispersal method unknown.

Number in parentheses refers to the number of motus in this area category.

* Not seen but possibly still present.

not been as poorly organized presents

TABLE 7

Widths of pioneer herb mats on seaward- and lagoon-facing shores, Caroline Atoll.

	<u>Average Width of Pioneer Herb Mat (m)</u>	
	Bordering Sea	Bordering Lagoon
Leeward Motus	18.5 (3-81)	4.2 (0-28)
Windward Motus	36.0 (24-69)	0.9 (0-3)

TABLE 8

Species-area relationships of six Pacific islands with entirely indigenous flora.

Island	Area	No. Species
Malden	39.3 sq km	9
Starbuck	16.2 sq km	6
McKean	57 ha	7
Phoenix	49 ha	6
Vostok	24 ha	3
Birnie	20 ha	4

Islands are arranged according to decreasing area. Data is from Garnett (1983), Fosberg and Sachet (n.d.), Clapp and Sibley (1971b), and pers. obs.

TABLE 9

Area of plant communities on the islets of Caroline Atoll.

	Area (ha)	Total Area (ha)
<u>Unvegetated Habitats</u>		41.39
Coral Rubble and Sand	41.39	
<u>Natural Plant Communities</u>		261.41
Natural Herb Mats	67.73	
Beach Scrub with <i>Suriana</i>	1.49	
<i>Pandanus</i> Forest ¹	3.38	
<i>Tournefortia</i> Scrub and Forest	125.25	
<i>Cordia</i> Forest ²	1.39	
<i>Pisonia</i> Forest	62.17	
<u>Anthropogenic Community</u>		96.14
Coconut Woodlands	96.14	
<u>Total Area Above High Water</u>		398.94

¹ Pure *Pandanus* only. Also mixed with *Pisonia*, *Tournefortia*, and *Cocos*.

² *Cordia*, where mixed with *Pisonia* and *Tournefortia*, is included in totals for those forest communities.

TABLE 10

Stature and extent of *Tournefortia* in the major habitats
of Caroline Atoll.

	Av. Hgt. (m)	Av. Width (m)	% <i>Tournefortia</i> Cover	No. Motus	No. Transects
Natural Herb Mat	1.4 (0.3–1.8)	49 (3–198)	25 (5–95)	14	20
<i>Tournefortia</i> Scrub & Forest	6 (0.3–15)	55 (2–287)	81 (5–100)	38	71
<i>Tournefortia</i> - <i>Pisonia</i> Forest	9.5 (5–15)	98 (8–284)	47 (5–90)	18	27

TABLE 11

Distribution of well-developed (≥ 10 m height) *Pisonia* forests on the motus
of Caroline Atoll.¹ Motus and transects are arranged according to the
decreasing height of their *Pisonia* groves. Capitals indicate those motus
whose forests were felled for *Cocos* plantations from 1916-20.

Motu & Transect	<i>Pisonia</i> Height (m)	Area of <i>Pisonia</i> (ha)	Motu Area (ha)
PIG	21*	3.36	7.21
NAKE, Transect 4	20*	20.79	107.46
Booby	20*	0.12	0.84
NORTH PIG	20*	1.83	5.44
NORTH BROTHERS	18*	0.43	1.71
NAKE, Transect 3 (central)	15*	20.79	107.46
LONG, Transect O	15*	15.00	75.98
BROTHERS	15*	0.37	4.31
Ana-Ana	15*	0.93	2.16
Danger	15*	0.39	2.71
NAKE, Transect 2	14*	20.79	107.46
Bird	14*	1.70	4.05
WINDWARD, Transect 2	14	2.97	11.42
Raurau	14*	1.07	3.48
CRESCENT	13	0.51	3.10
Mannikiba, Transect 1	12*	1.13	21.49
Shark	12	2.60	7.98
NAKE, Transect 3 (west)	12	20.79	107.46
LONG, Transect 12	12	15.00	75.98
<i>Pisonia</i>	11*	0.86	2.45
Matawa	11	0.07	1.71
Nautonga	11	0.02	0.34
NAKE, Transect 3 (southwest)	11	20.79	107.46
Kimoa	11	0.59	1.80
Emerald	11	3.20	8.34
Eitei	11	0.38	1.42
LONG, Transect B	10	15.00	75.98
LONG, Transect 8	10	15.00	75.98
NAKE, Transect 1	10	20.79	107.46
WINDWARD, Transect 1	10	2.97	11.42
Blackfin	10	0.41	2.62
NORTH ARUNDEL	10	0.18	0.91

¹ *Tournefortia* or *Cordia* may be present, but sub-dominant to *Pisonia*.

* 90–100% canopy cover.

· 50–80% canopy cover.

TABLE 12

Area and Dimensions of *Pisonia grandis* on Vostok, Flint, and five islets of Caroline Atoll.

Island/Islet	Area of <i>Pisonia</i> ha	No. trees or main trunks	Mean Height (m)	Range of Heights (m)	Mean cbh ¹ (m)	Range of cbh (m)	Mean base ² (m)	Range of base circumferences (m)
CAROLINE	62.17							
North Pig	1.83	25	19	11-21	221	110-359	261	205-470
Brothers	0.37	10	15	15	140	50-219	243	154-340
Pig	3.36	5	16	12-17	338	290-660	282	230-333
North Brothers	0.43	3	18	18			314	293-332
Long	15.00	3	15	15			414	282-500
Total for above islets at Caroline	20.99	46	18	11-21	213	50-660	293	154-500
VOSTOK	13.5	58	18	10-25	218	67-510		
FLINT	approx. 4 (fragmented)	20	17	8-30	160	60-200	598	100-1000

¹ cbh = circumference at 1.5 m.² base = base circumference at 0.3 m.

TABLE 13

Number of trees and areas planted in *Cocos* on Caroline's islets during the major planting era (1916-1920), also showing remnant *Cocos* data for 1990.

Islet	Islet Area (ha)	Area Forest of Scrub Usable for <i>Cocos</i> in 1990 ¹ (ha)					1916-20		Approx. % 1990	
							Approx.		Forest	
		<i>Tourn.</i>	<i>Pis.</i>	Other	<i>Cocos</i>	Total	No. <i>Cocos</i> Planted	Area <i>Cocos</i> ² (ha)	% <i>Cocos</i> 1990	Planted in <i>Cocos</i> 70 Yrs Ago
South	104.41	4.20	0	1.10	80.00	86.10	13,006	94.90	477	100%
Nake	107.46	30.65	20.8	9.41	5.75	66.61	10,544	76.97	6	100%
Long	75.98	32.20	15.00	-	2.40	49.60	1,343	9.80	3	20%
Tridacna (A1) ³	9.08	7.97	0	0.18		8.15	910	6.64	0	82%
Arundel	7.34	4.36	0.95	-	0	5.31	646	4.71	0	89%
N. Arundel (A2)	0.91	0.33	0.19	-	few trees	0.52	69	0.50	0	100%
Brothers	4.31	2.00	0.37	-	0.01	2.38	315	2.30	0.2	97%
N. Brothers (A3)	1.71	0.68	0.43	-	few trees	1.11	180	1.31	0	100%
Pig	7.25	1.61	3.36	-	0.03	5.00	538	3.93	0.4	79%
N. Pig (A4)	5.44	1.31	1.84	-	0	3.15	402	2.93	0	93%
Crescent (A5)	3.10	1.56	0.51	-	0	2.07	228	1.66	0	80%
Windward (A6)	11.42	5.70	2.97	-	0	8.67	1,299	9.48	0	100%
								215.10		

¹ "Usable area" does not include unvegetated rubble or natural herb mats.² Based on Caroline's planting densities of 28 × 28 sq ft (Young ca. 1922).³ The "A" series of islet names are from Young (ca. 1922).

TABLE 14

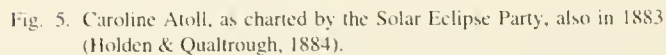
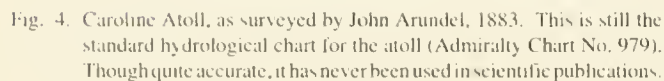
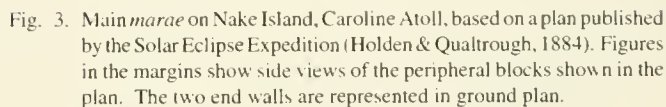
Species diversity in *Pisonia* forests of decreasing maturity, Caroline Atoll. Motus are arranged according to the degree of coverage of their constituent *Pisonia* trees; within these groupings, the motu order is dependent upon the total number of plant species within this same habitat. Note that there is an inverse relationship between the purity of the true *Pisonia* forest and species diversity.

Canopy Cover	Av. Canopy Hgt. (m)	Av. No. Spp. (incl. <i>Pisonia</i>)	Total Numbers of Species			No. Transects
			Trees	Shrubs	Herbs	
100% (<i>Pisonia</i> only)	13	1	1	0	0	1
100% (co-dominant present)	15	3.4	2	0	5	9
90–95%	10	5.2	5	1	7	9
50–90%	10	6.2	5	2	7	15
25–50%	7	6.2	4	1	6	5
<25% ¹	9	5.63	3	2	9	6
Motus with one <i>Pisonia</i> tree only	6	4.0	3	1	3	2

¹ South Island not included, as its *Pisonia* is too rare and fragmented.



Fig. 1. Line Islands: geographic location in the Pacific Ocean.



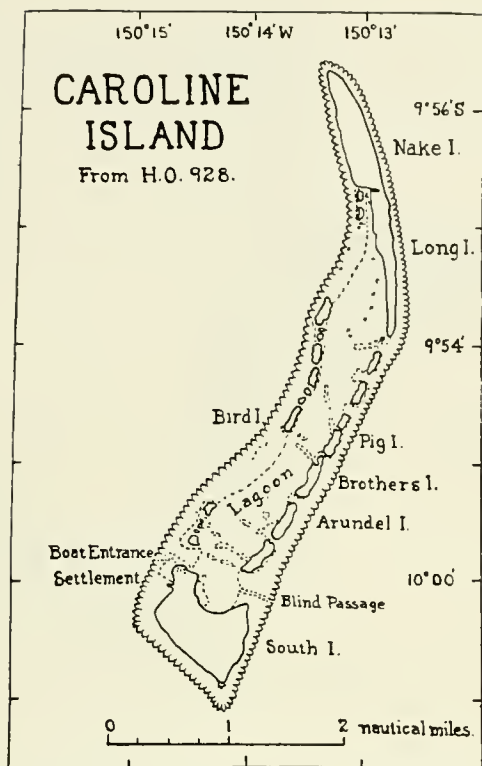


Fig. 6. Caroline Atoll, a modified version of the Solar Eclipse Party's map (1883) as portrayed by Bryan (1942). Though highly inaccurate, modifications of this map have been used in all publications since Bryan (1942).

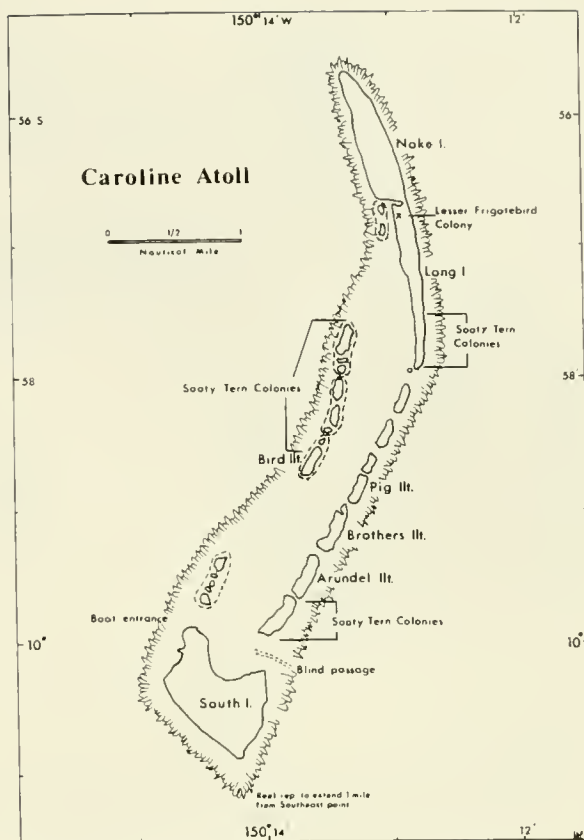


Fig. 7. This map, by Clapp & Sibley (1971a), was based on Fig. 6.



Fig. 8. Caroline Atoll: survey transects. The distance covered was 13.3 km.

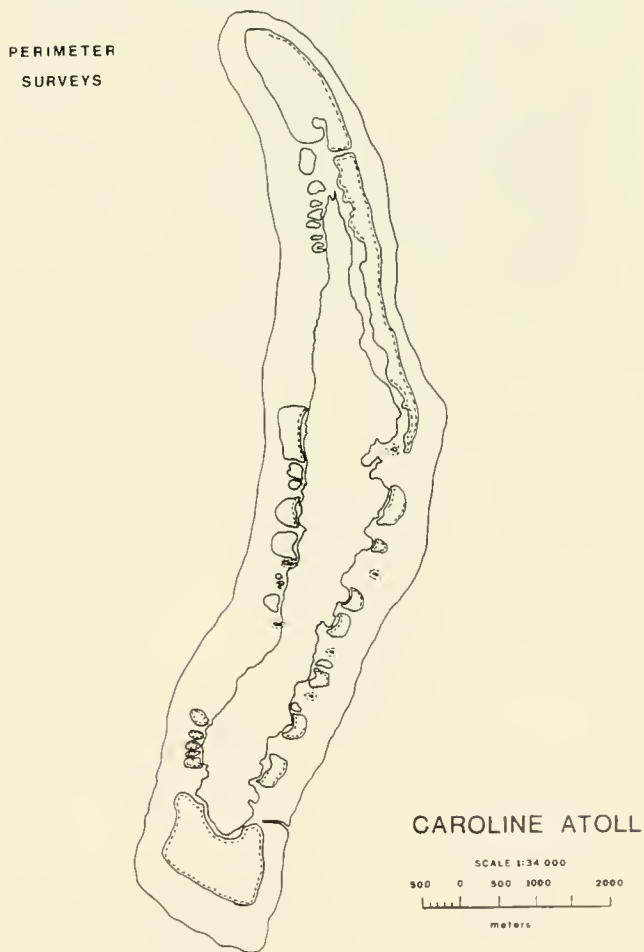


Fig. 9. Caroline Atoll: perimeter surveys. The distance covered was 19.3 km.

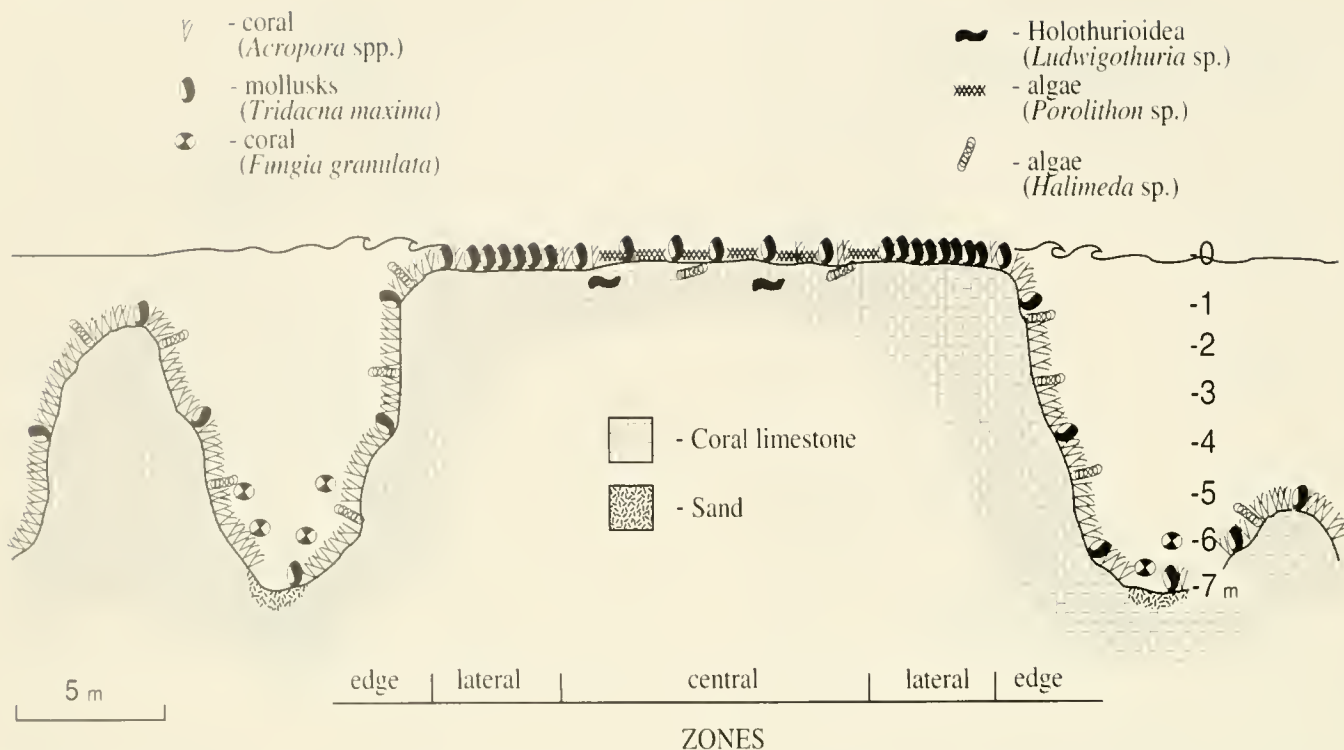


Fig. 10. Diagrammatic representation of a portion of the outstanding *Acropora-Tridacna* reefs connecting the islets Ana-Ana, Kimoa and Tridacna. Giant clams (*Tridacna maxima*), thickly studding the reef, attain densities of 80 per square meter (Sirenko & Koltun, Subchapter 1.4).



Fig. 11. Entire distribution map of rare and/or localized plants on Caroline Atoll: *Hibiscus tiliaceus*, *Lepidium bidentatum*, *Pandanus tectorius*, *Phyllanthus amarus*, *Psilotum nudum*, *Scaevola sericea*, *Sida fallax*, *Tacca leontopetaloides*, *Thespesia populnea*, *Tribulus cistoides*, *Ximenia americana*, and Species A. *Psilotum* may still exist on Nake.

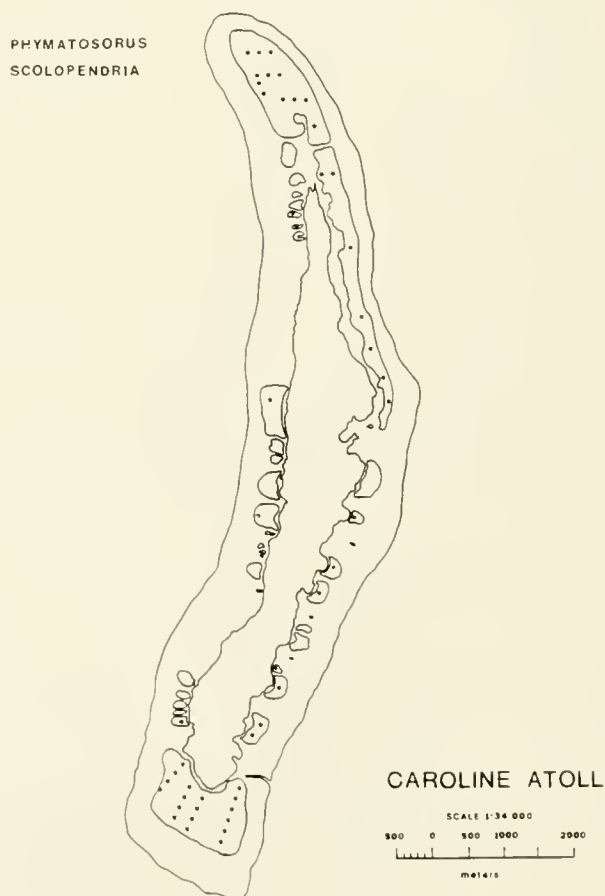


Fig. 12. Transect distribution map of the fern *Phymatosorus scolopendria* on Caroline Atoll.

LEPTURUS REPENS



Fig. 13. Transect distribution map of the grass *Lepturus repens* on Caroline Atoll. Arrows indicate areas of highest density.

COCOS NUCIFERA

- Healthy Cocos
- Dying Cocos - Ipomoea Forest
- Mixed Forest
- Isolated groves



Fig. 14. Entire distribution map of the coconut *Cocos nucifera* on Caroline Atoll.

LAPORTEA RUDERALIS

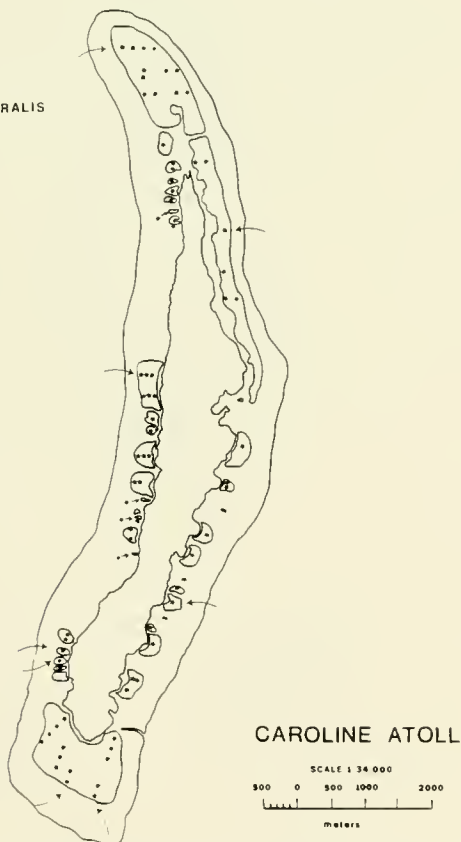


Fig. 15. Transect distribution map of *Laportea ruderalis* on Caroline Atoll. Arrows indicate areas of highest density.

ACHYRANTHES CANESCENS



Fig. 16. Transect distribution map of *Achyranthes canescens*. Arrows indicate areas of highest density.



Fig. 17. Transect distribution map of pigvine, *Boerhavia repens*, Caroline Atoll. Arrows indicate areas of highest density.



Fig. 18. Entire distribution map of the buka tree, *Pisonia grandis*, Caroline Atoll. Arrows indicate forests from 10 to 21 m tall.



Fig. 19. Transect distribution map of the succulent herb *Portulaca lutea*, Caroline Atoll. Arrows indicate pure *Portulaca* flats.



Fig. 20. Transect and perimeter survey distribution map of *Suriana maritima*. Arrows indicate areas of highest density.

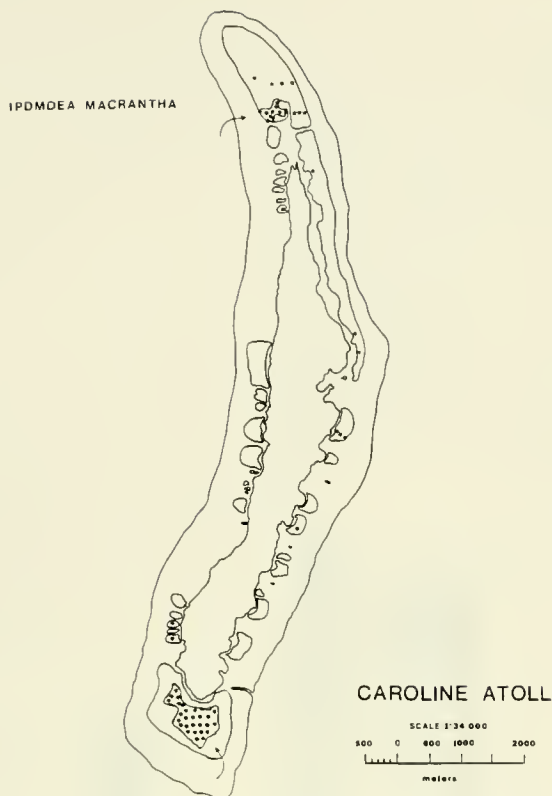


Fig. 21. Transect distribution map of *Ipomoea macrantha*. Entire distribution is shown for South and Nake Islands. Arrows indicate areas having significant amounts of this vine.

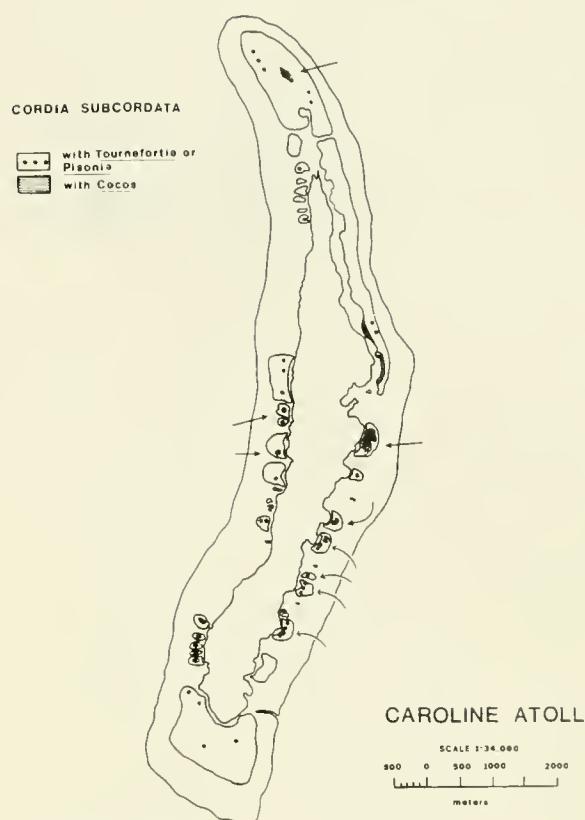


Fig. 22. Entire distribution map of *Cordia subcordata*. Arrows indicate small, but monotypic, stands.

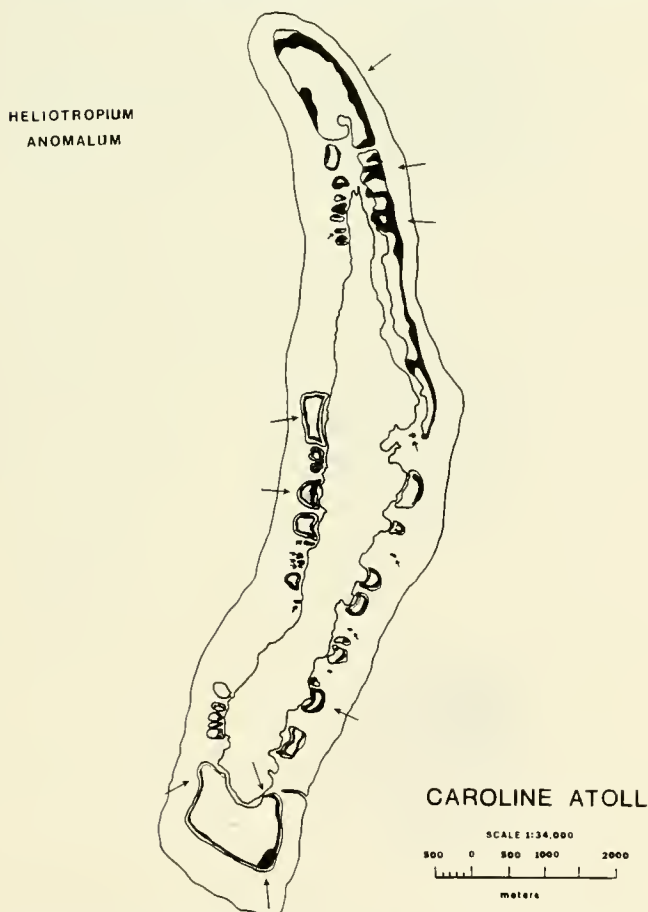


Fig. 23. Entire distribution map of *Heliotropium anomalum*. Arrows indicate areas of highest density.

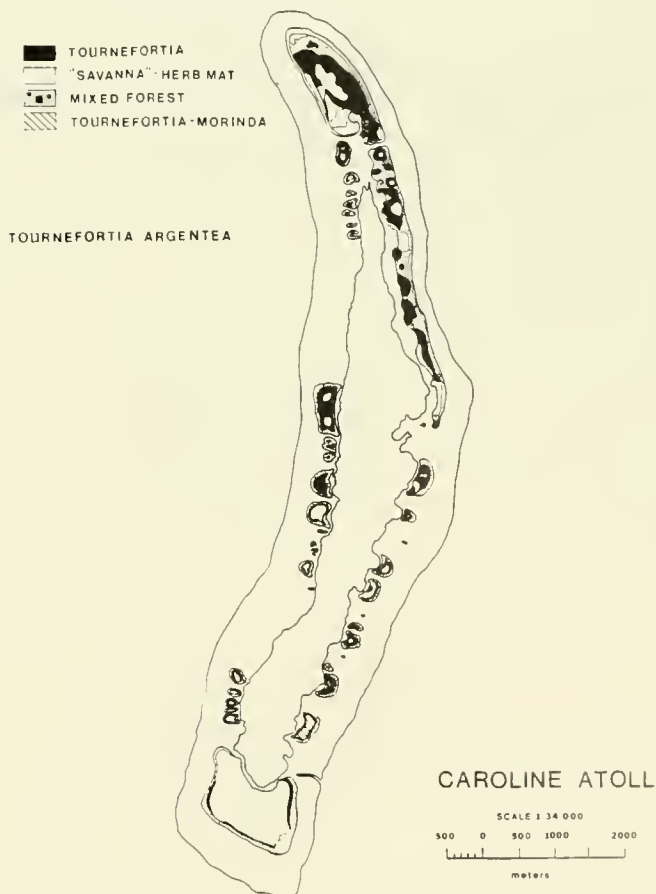


Fig. 24. Entire distribution map of *Tournefortia argentea*. Because this shrub dominates Caroline's woodlands, there are no individual arrows to indicate areas of high density.



Fig. 25. Transect distribution map of *Morinda citrifolia*. The outlined area on Tridacna Islet (northeast of South Island) encloses *Tournefortia-Morinda* forest. Arrows indicate areas of highest density.

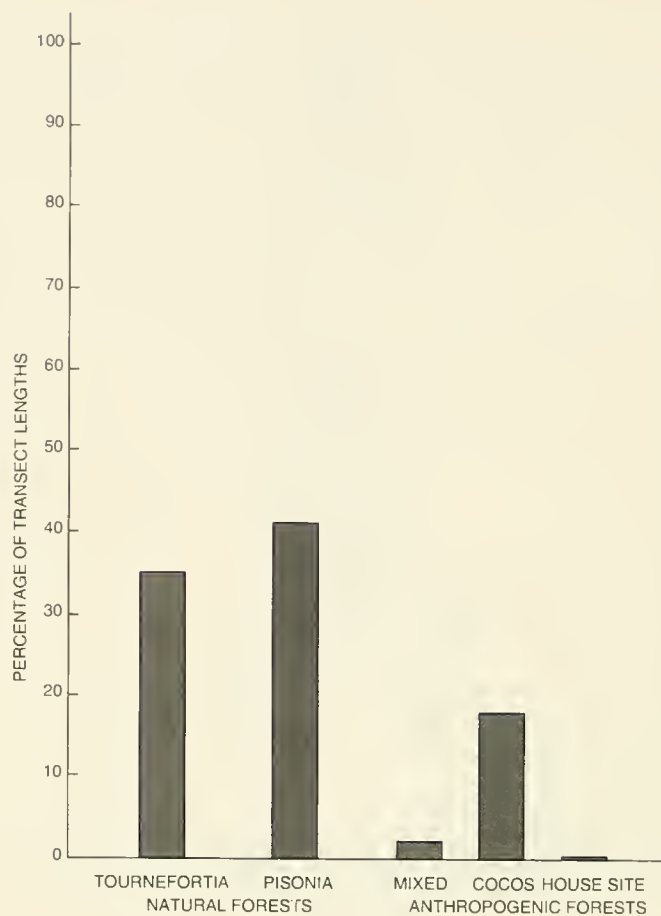


Fig. 26. Evidence for the indigenous status of *Morinda citrifolia* on Caroline Atoll: percentage cover on transects within natural and anthropogenic forests. *Morinda* occurs on 30 (77%) motus, never in a "planted" situation.

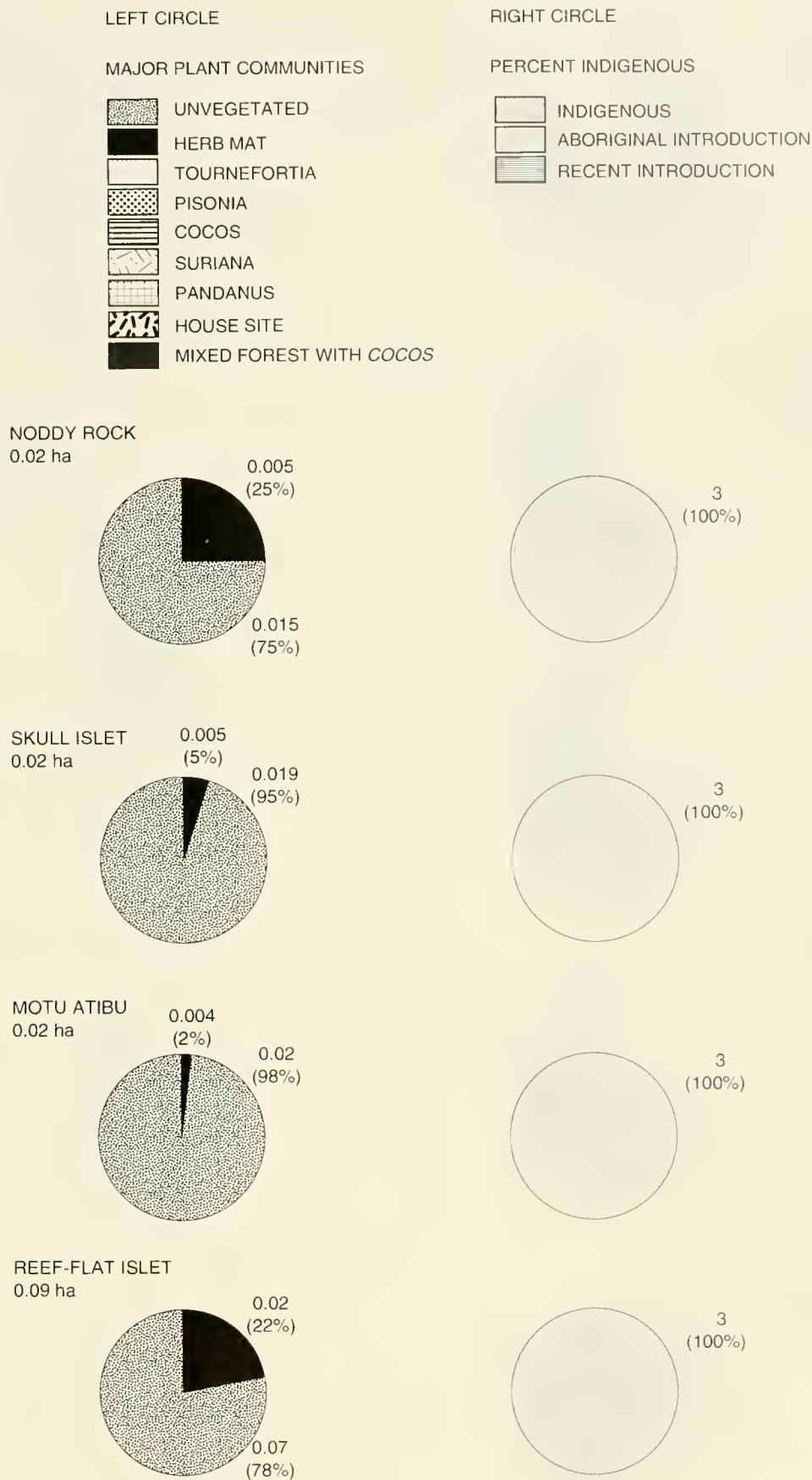


Fig. 27. Plant communities and amount of indigenous vegetation on motus less than 0.1 ha, Caroline Atoll. The left "pie" depicts the relative amount of a motu's total surface area covered by each plant community; numbers indicate actual area in hectares. The right "pie" depicts the numbers and percentages of indigenous and anthropogenic species per motu. Data is based on the vegetation maps for each motu (Figs. 37-57) and Tables 2 and 9.

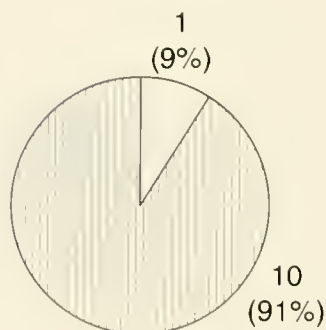
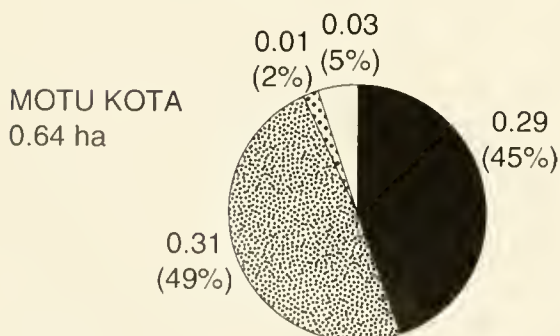
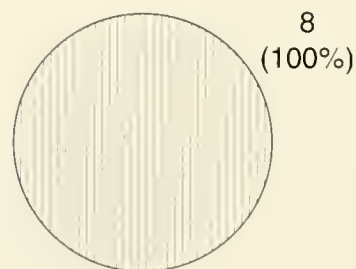
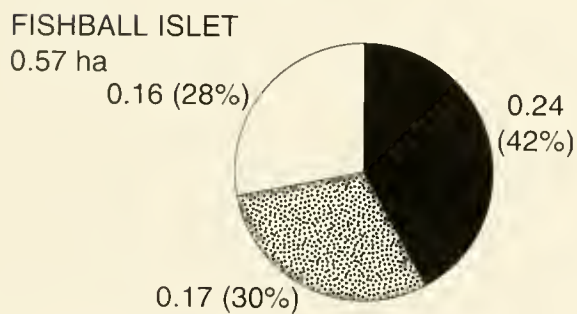
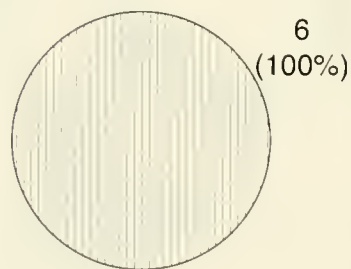
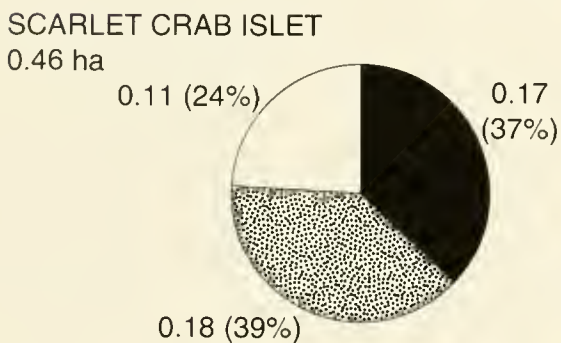
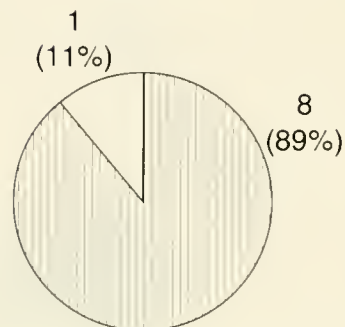
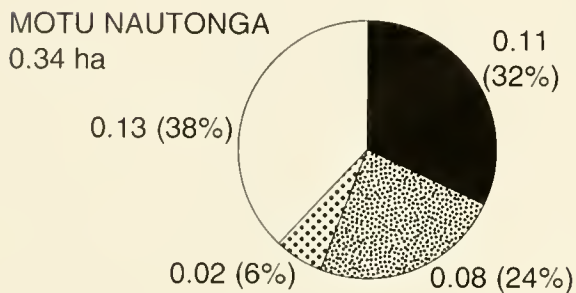
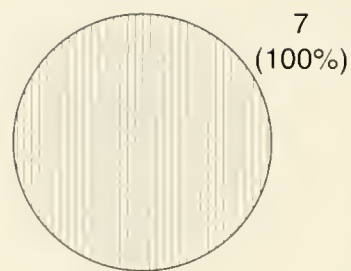
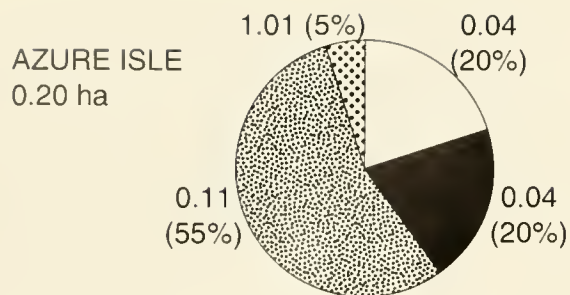
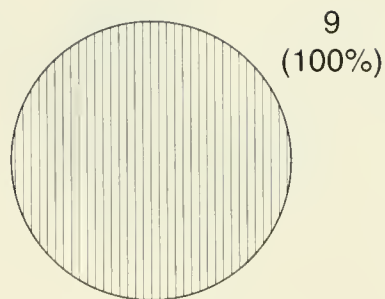
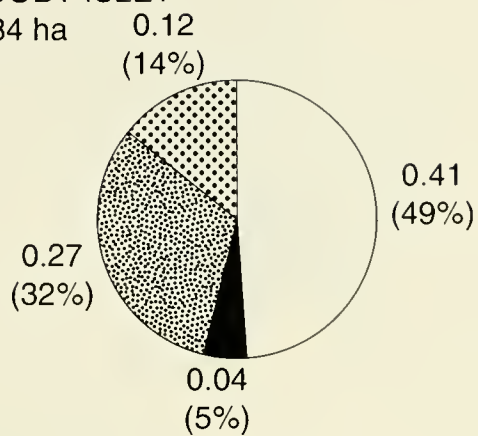


Fig. 28. Plant communities and amount of indigenous vegetation on motus 0.2 to 0.7 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

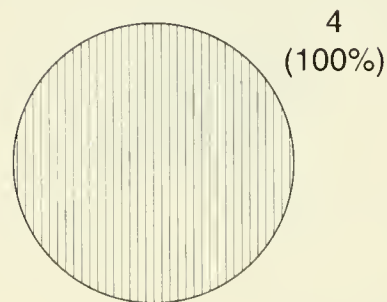
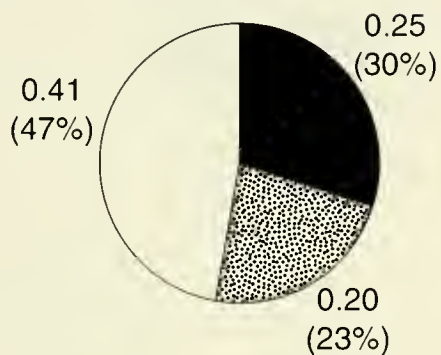
BOOBY ISLET

0.84 ha



BO'SUN BIRD ISLET

0.86 ha



NORTH ARUNDEL ISLET

0.91 ha

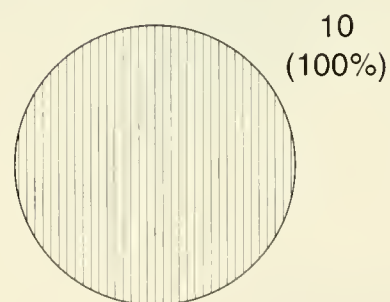
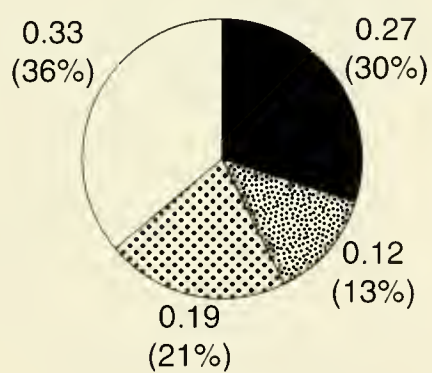
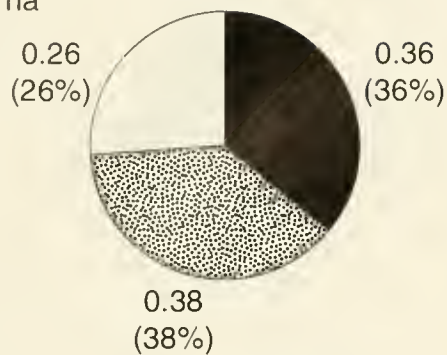


Fig. 29a. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

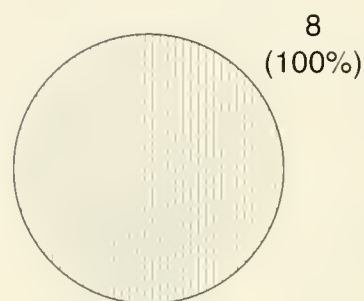
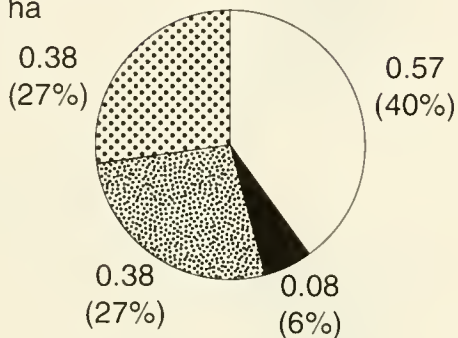
MOTU MOUAKENA

1.00 ha



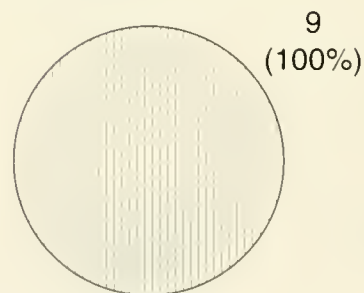
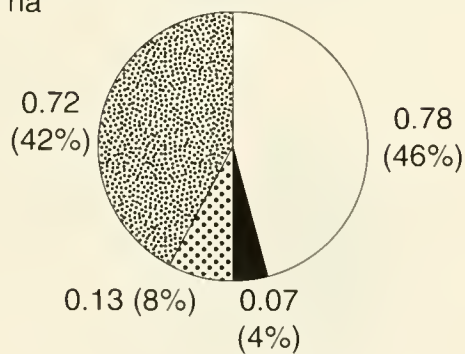
MOTU EITEI

1.41 ha



CORAL ISLET

1.07 ha



MOTU MATAWA

1.71 ha

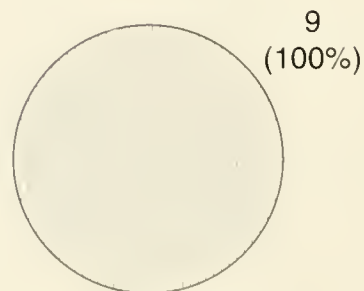
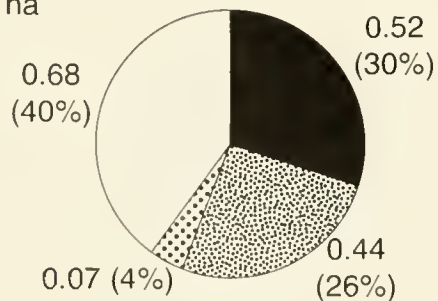
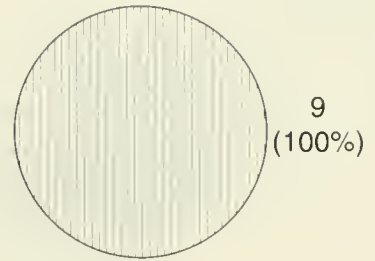
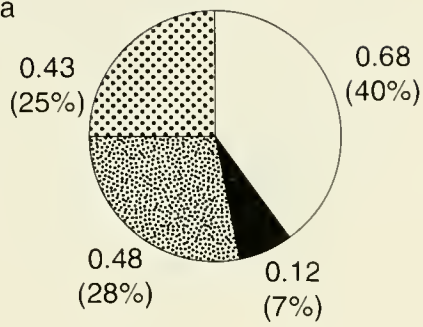


Fig. 29b. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

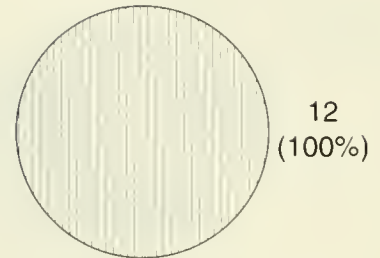
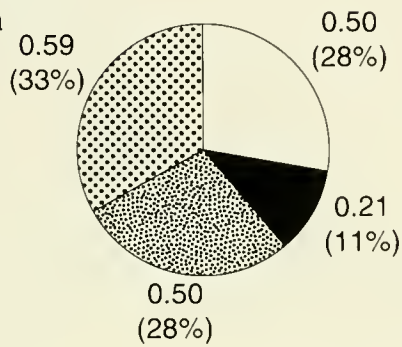
NORTH BROTHERS ISLET

1.71 ha



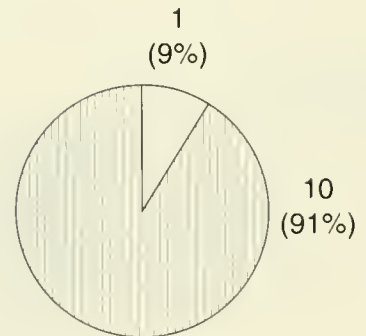
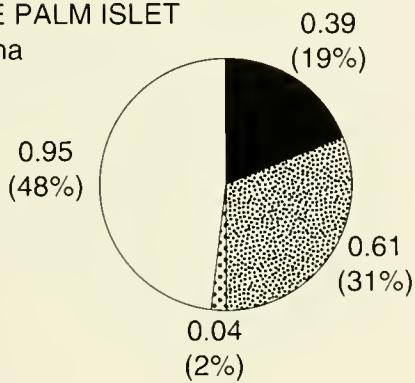
MOTU KIMOA

1.80 ha



LONE PALM ISLET

1.99 ha



MOTU ANA-ANA

2.16 ha

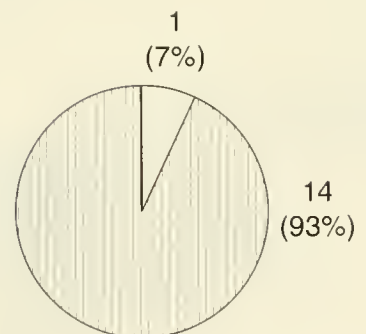
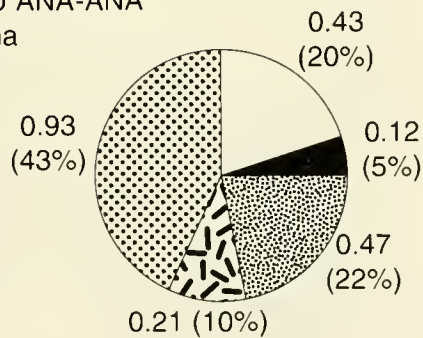
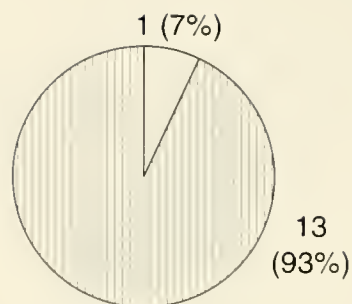
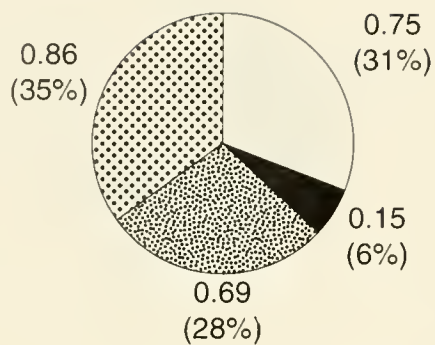


Fig. 29c. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

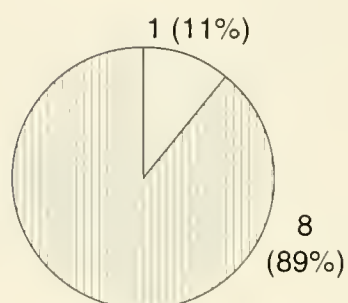
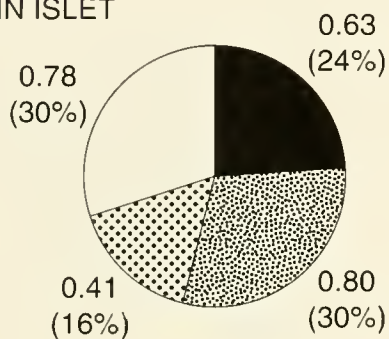
PISONIA ISLET

2.45 ha



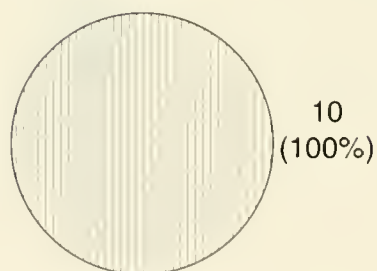
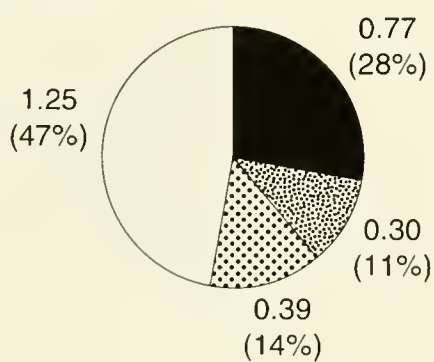
BLACKFIN ISLET

2.62 ha



DANGER ISLET

2.71 ha



CRESCENT ISLET

3.10 ha

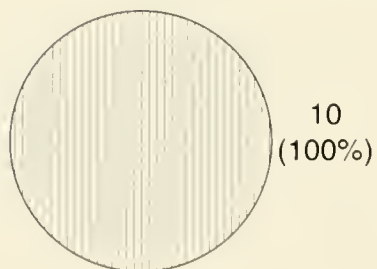
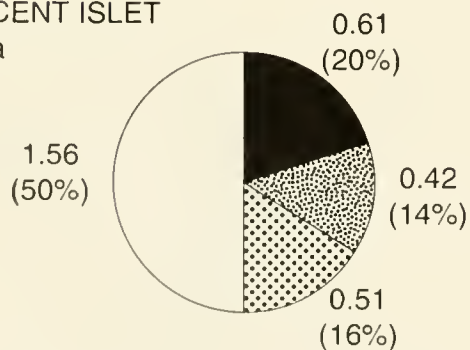
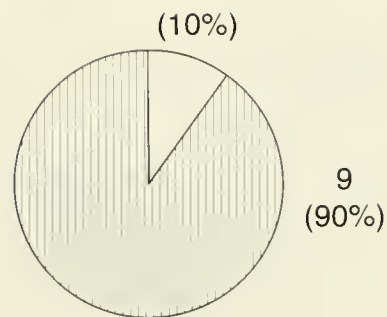
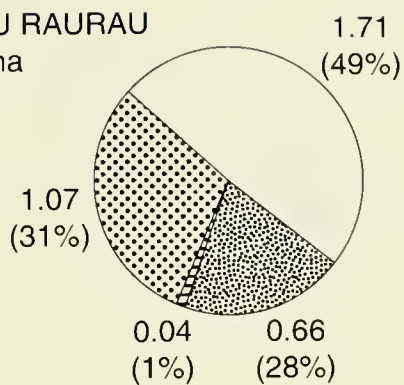
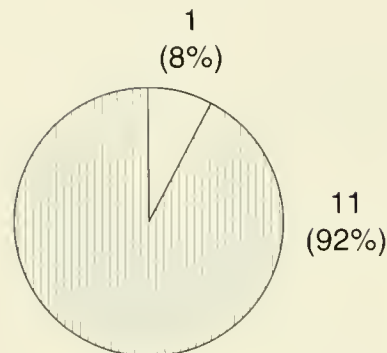
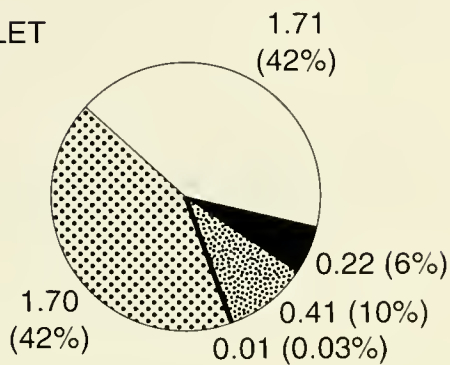


Fig. 29d. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

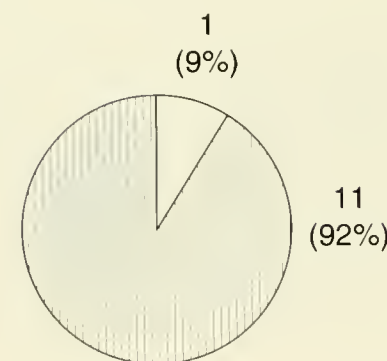
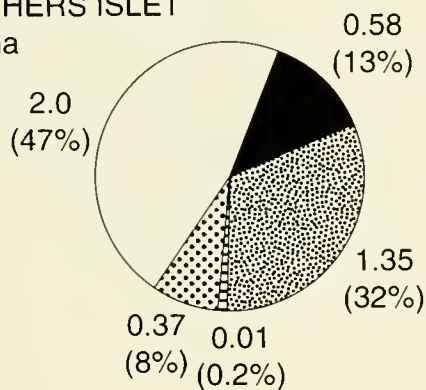
MOTU RAURAU
3.48 ha



BIRD ISLET
4.05 ha



BROTHERS ISLET
4.31 ha



NORTH PIG ISLET
5.44 ha

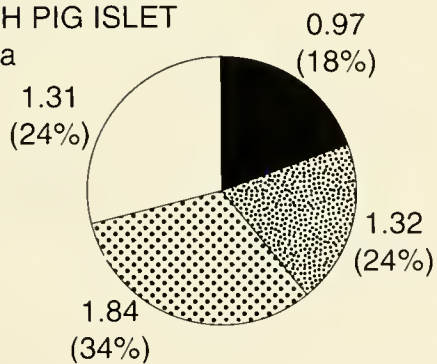


Fig. 29e. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

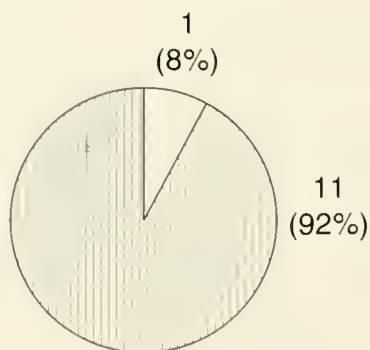
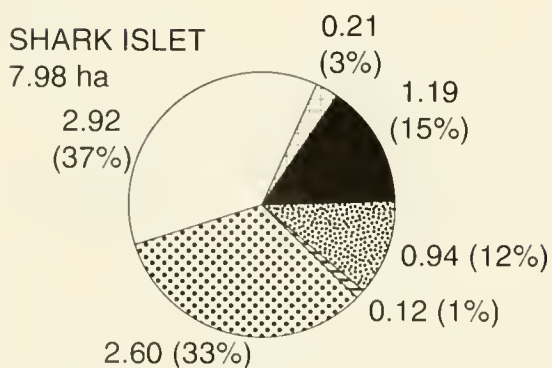
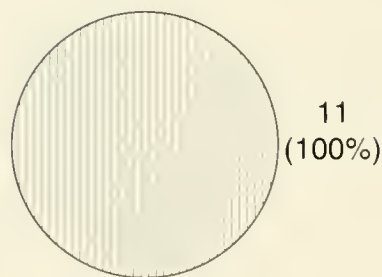
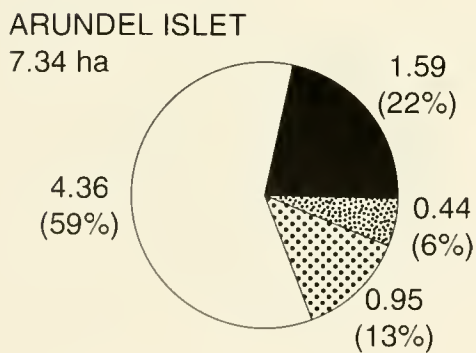
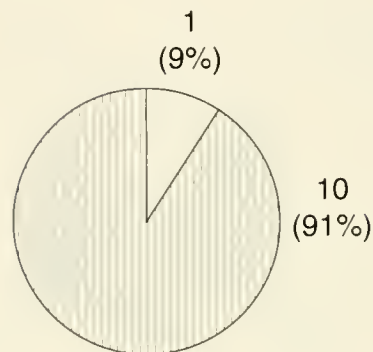
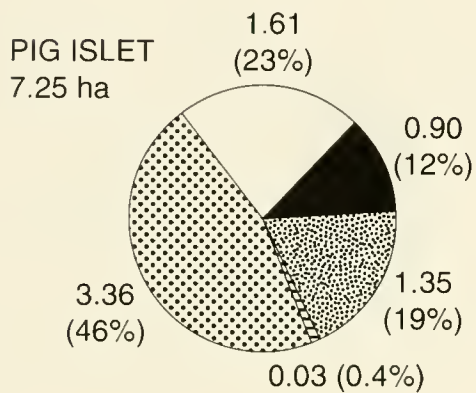
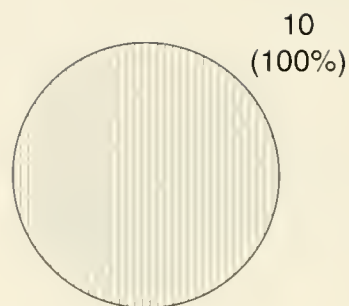
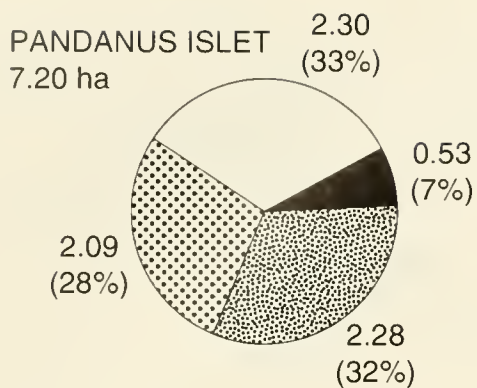


Fig. 29f. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

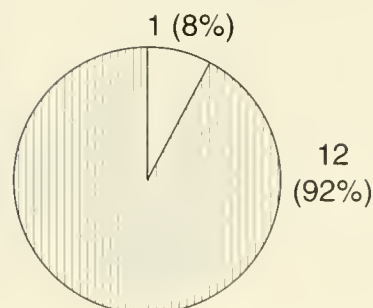
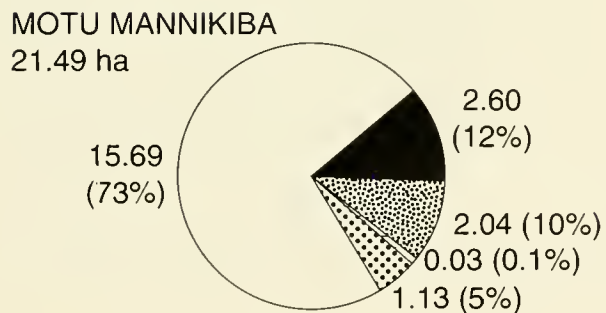
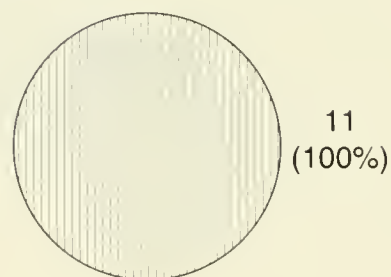
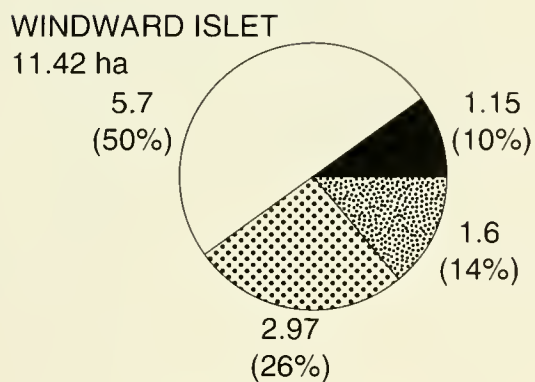
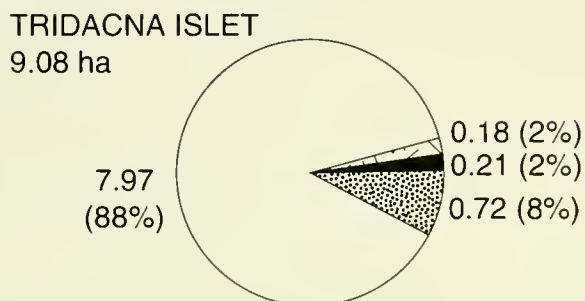
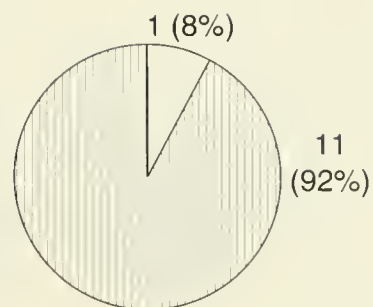
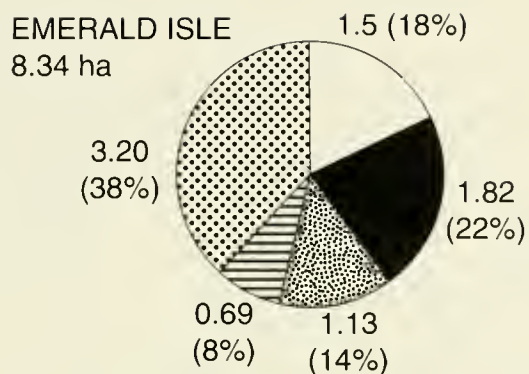
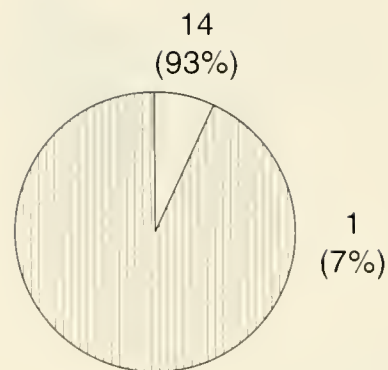
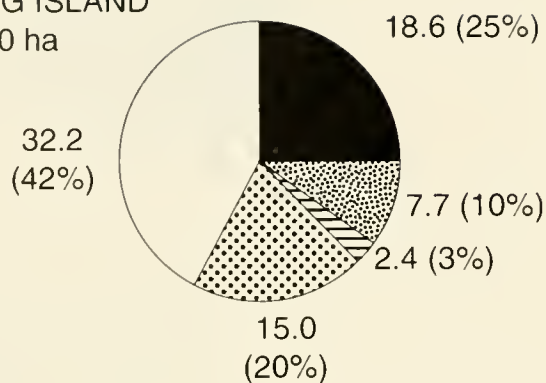
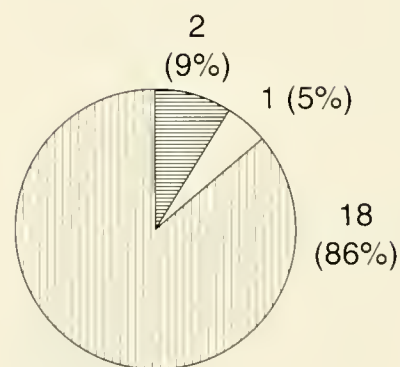
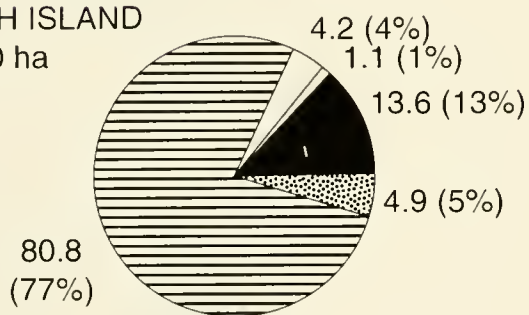


Fig. 29g. Plant communities and amount of indigenous vegetation on motus 0.8 to 25.0 ha, Caroline Atoll. See Fig. 27 for explanation of the figure.

LONG ISLAND
75.90 ha



SOUTH ISLAND
104.60 ha



NAKE ISLAND
91.71 ha

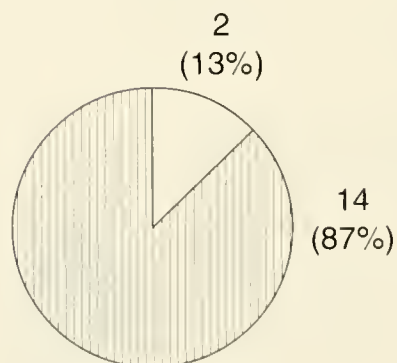
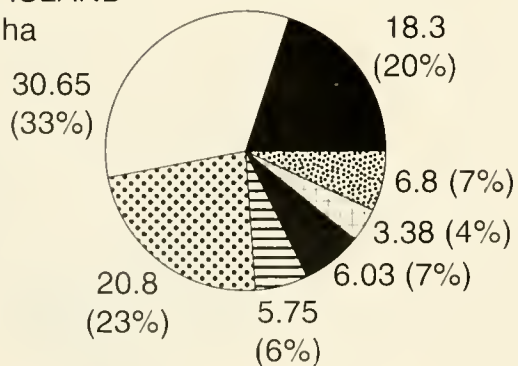


Fig. 30. Plant communities and amount of indigenous vegetation on motus over 25.0 ha. See Fig. 27 for explanation of the figure.

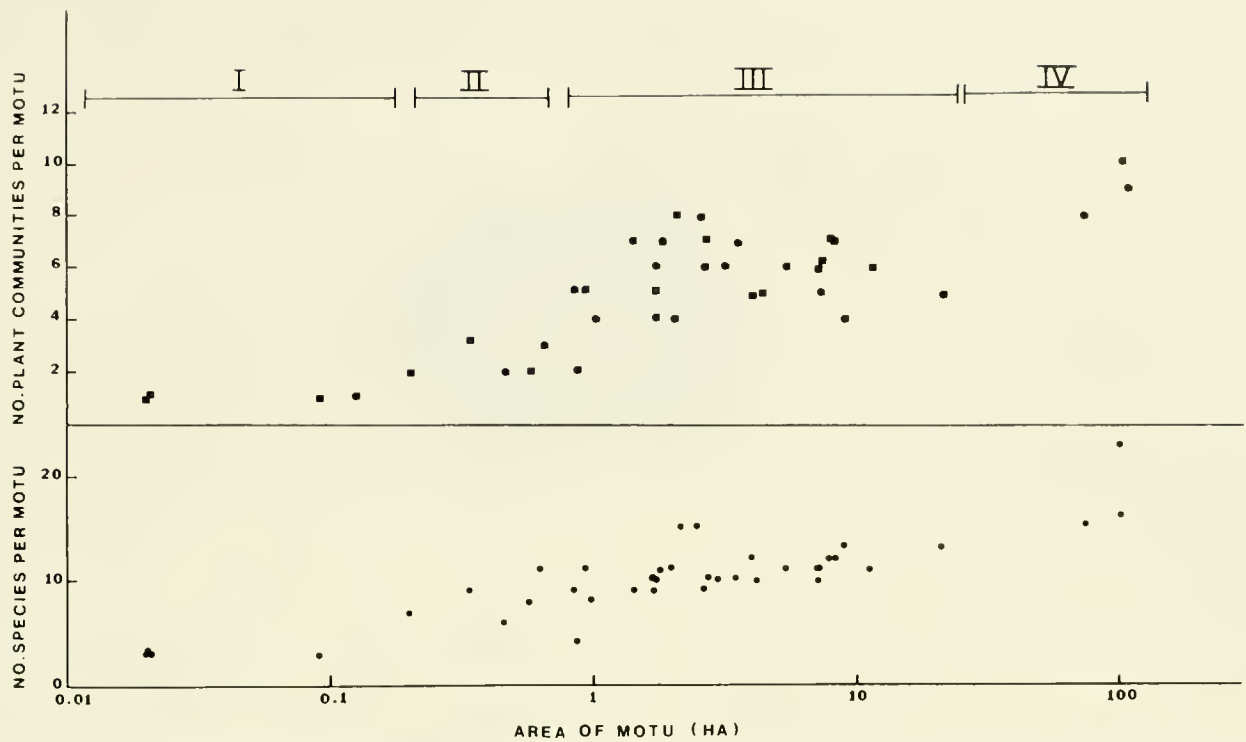


Fig. 31. Total numbers of plant communities (upper graph) and species (lower graph) in relation to islet area, demonstrating plant succession on the differentsized islets encircling Caroline's lagoon. Roman numerals refer to size classes of the motus: I = < 0.2 ha, II = 0.2 to 0.7 ha, III = 0.8 to 25.0 ha, IV = > 25.0 ha. The break between II and III marks a substantial increase in the diversity, area coverage, and height of the forest ecosystems. Data is based on Table 5.

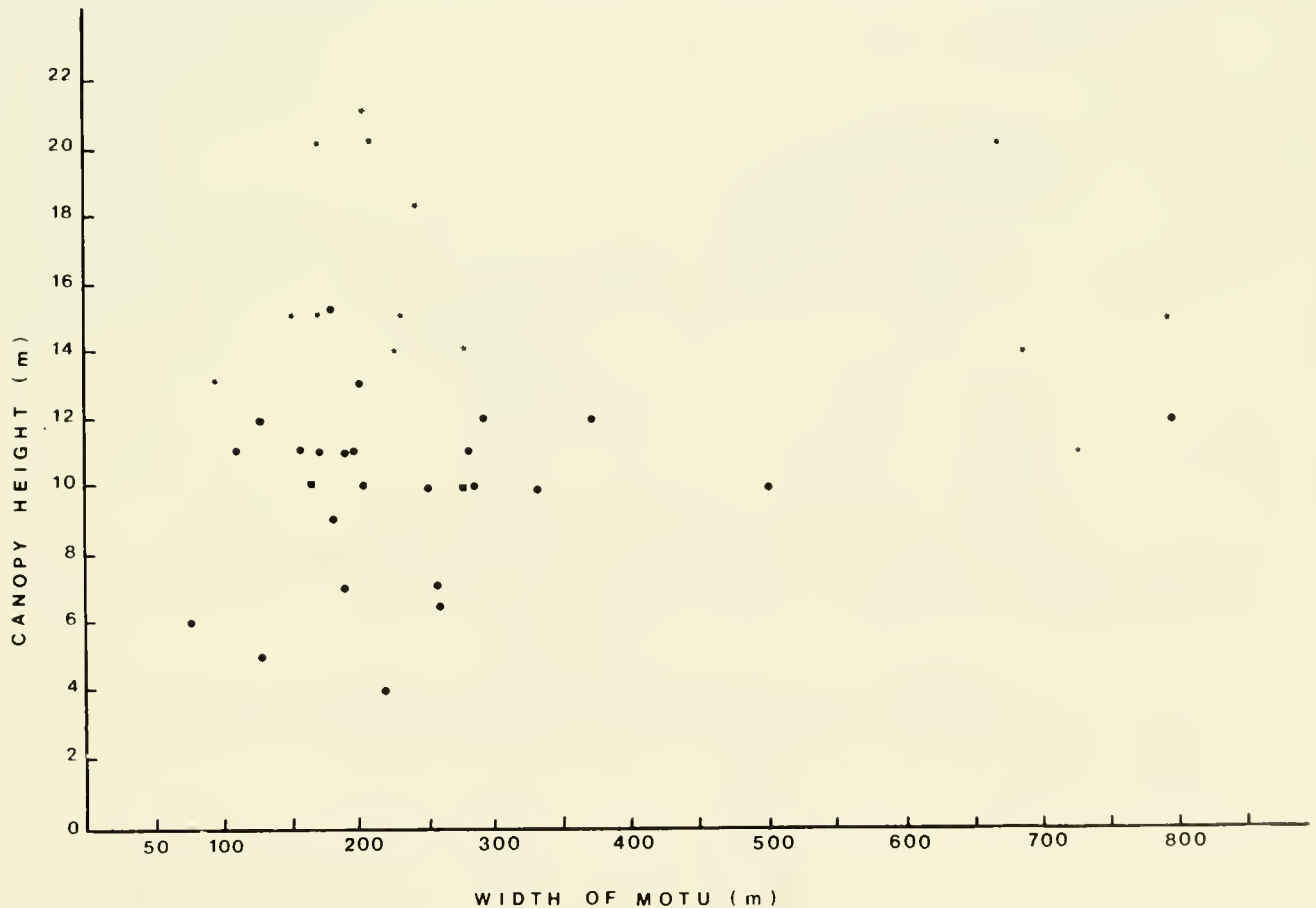


Fig. 32. Maximum heights of *Pisonia* forests in relation to width of the motus. Stars represent forests with 90–100% canopy cover; dots represent forest or scrub with less than 90% cover.

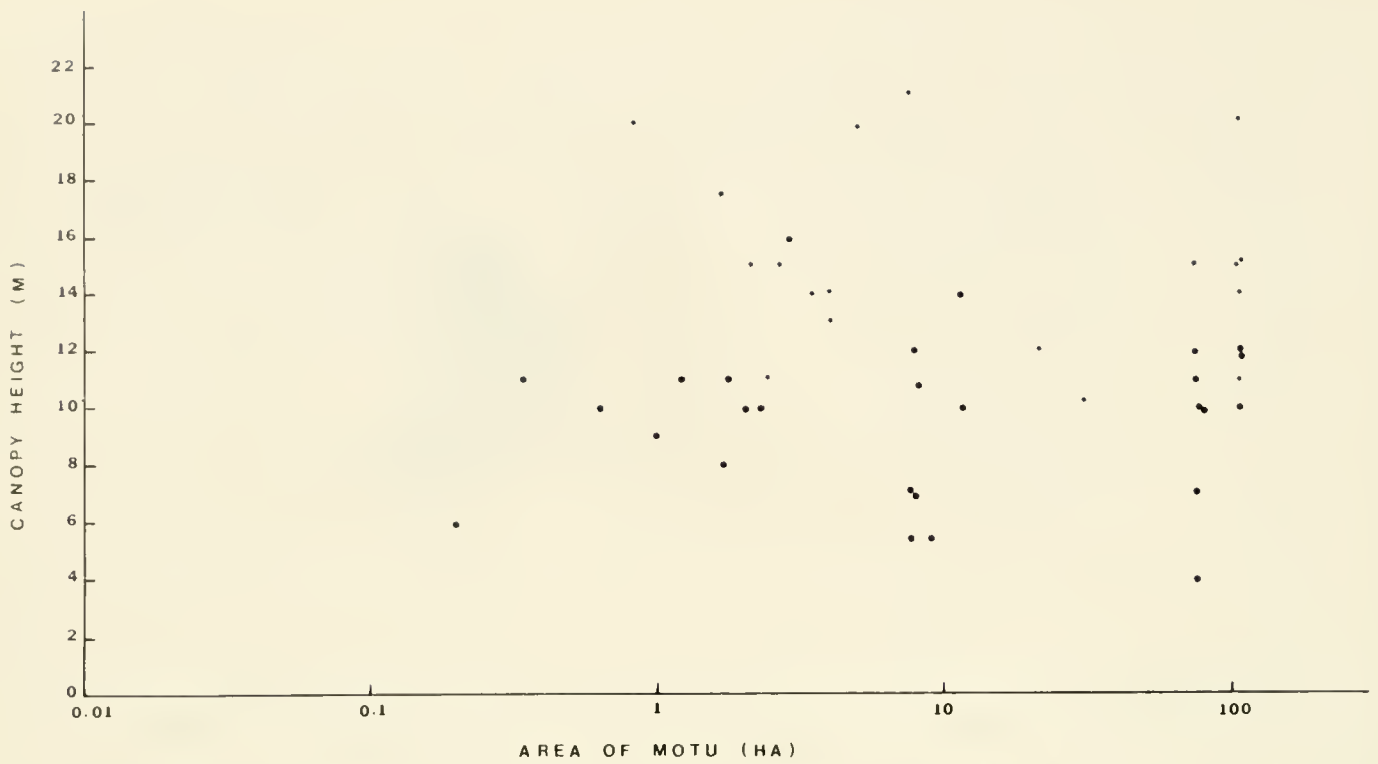


Fig. 33. Maximum canopy heights of *Pisonia* forests in relation to islet area. Stars represent forests with 90–100% canopy cover; dots represent forest or scrub with less than 90% cover.



Fig. 34. Schematic profile through Arundel Islet, recovering from disturbance over 60 years ago, showing natural herb mats, *Tournefortia* scrub and forest, and five species of breeding seabirds. Vertical height is exaggerated.

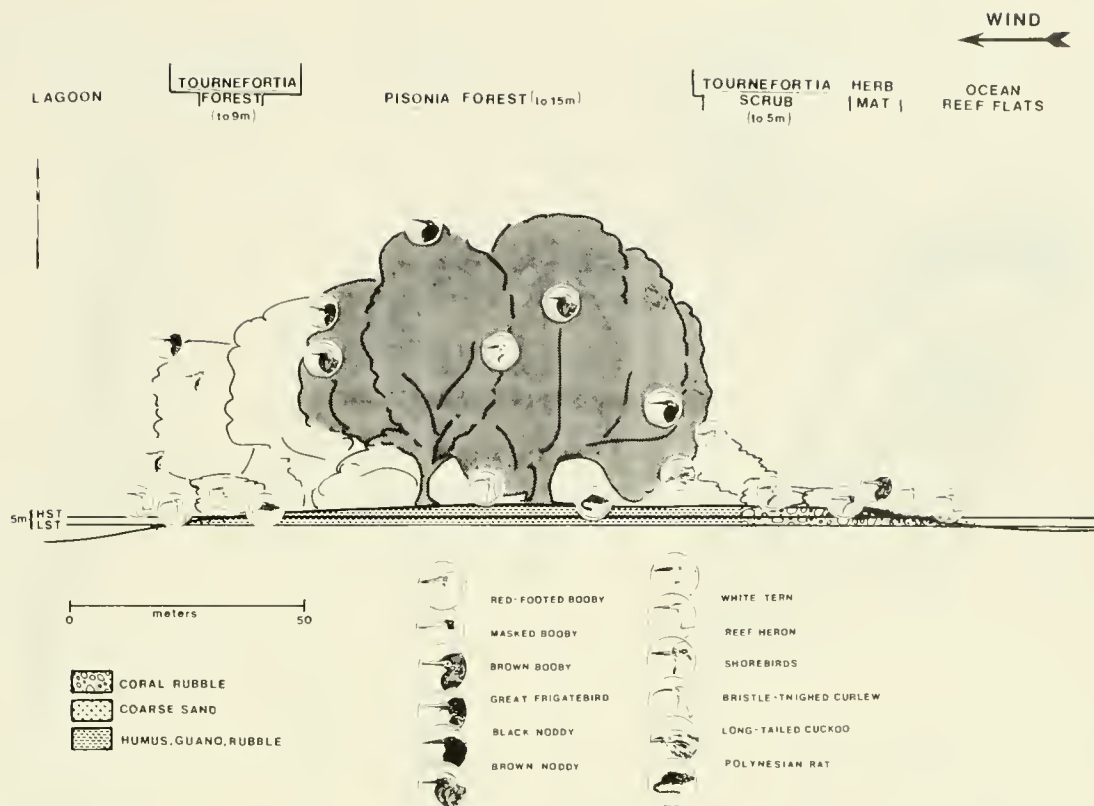


Fig. 35. Schematic profile through Long Island, Tr. O. Although Long Island has been formed in the recent past by a merger of five smaller islets, this section of the islet is very mature, containing natural herb mats, *Tournefortia* scrub and forest, and tall *Pisonia* forest. Seven species of seabirds breed. Vertical height is exaggerated.

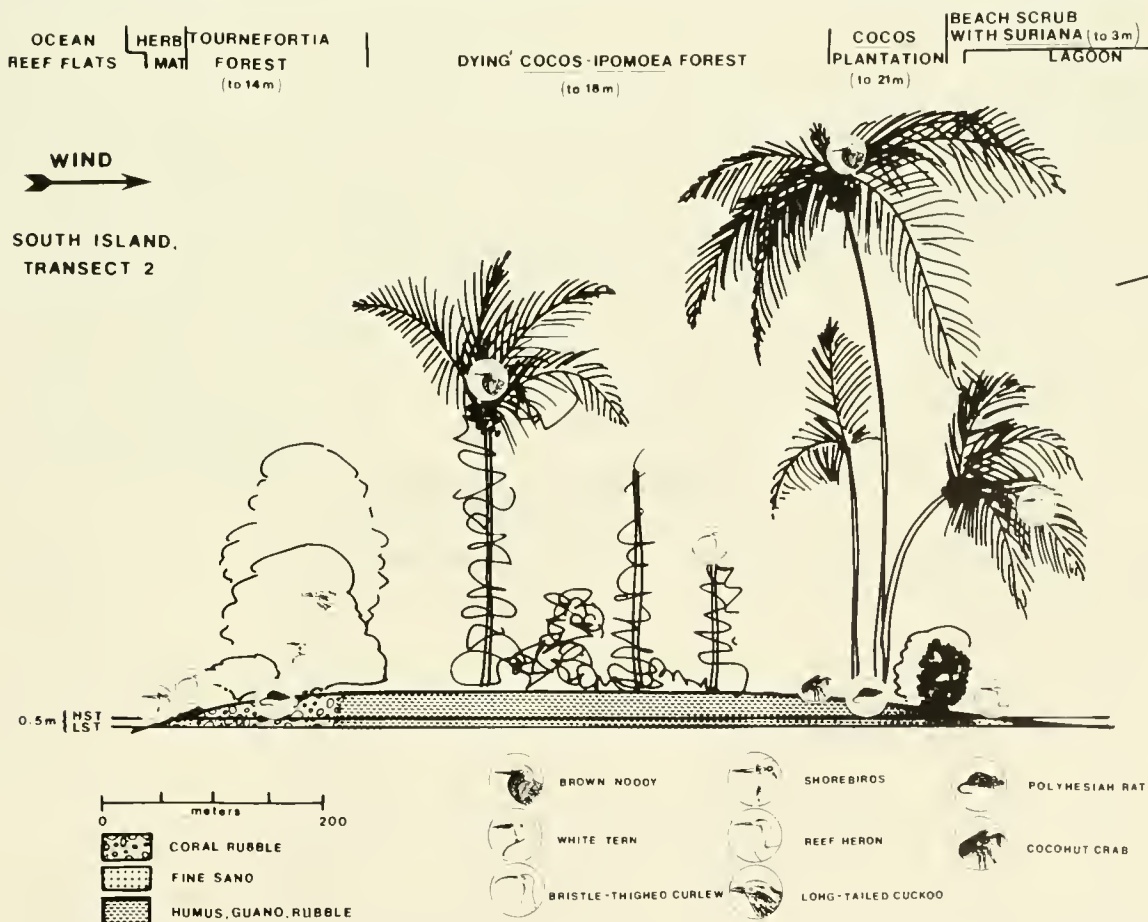


Fig. 36. Schematic profile through South Island, where 77% of the land surface is covered with *Cocos* forests, primarily in a dying state. Vertical height is exaggerated.

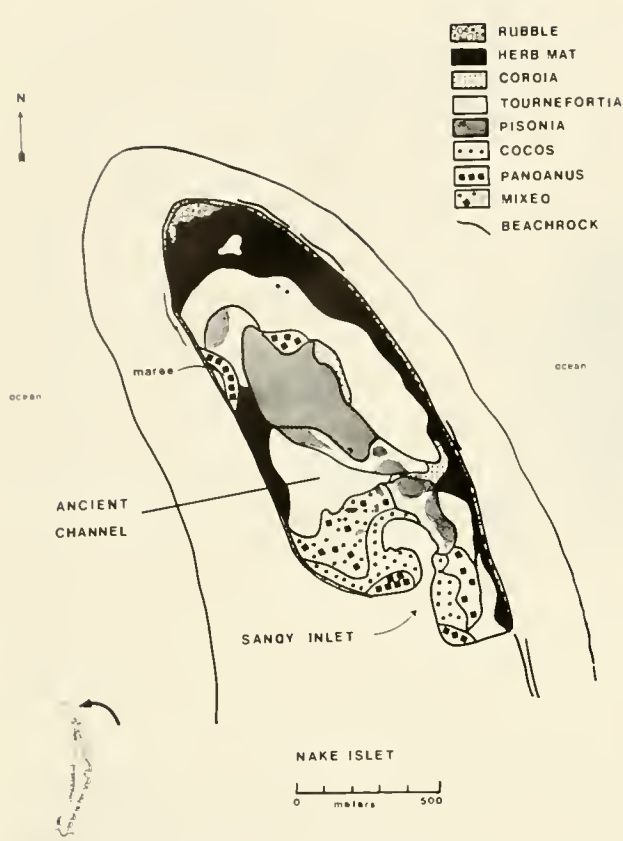


Fig. 37. Nake Island: vegetation and physiography.

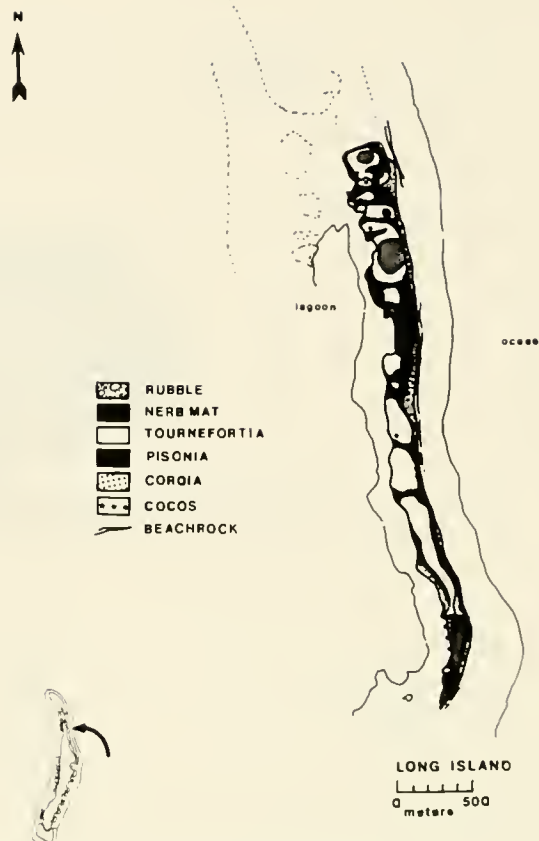


Fig. 38. Long Island: vegetation and physiography.

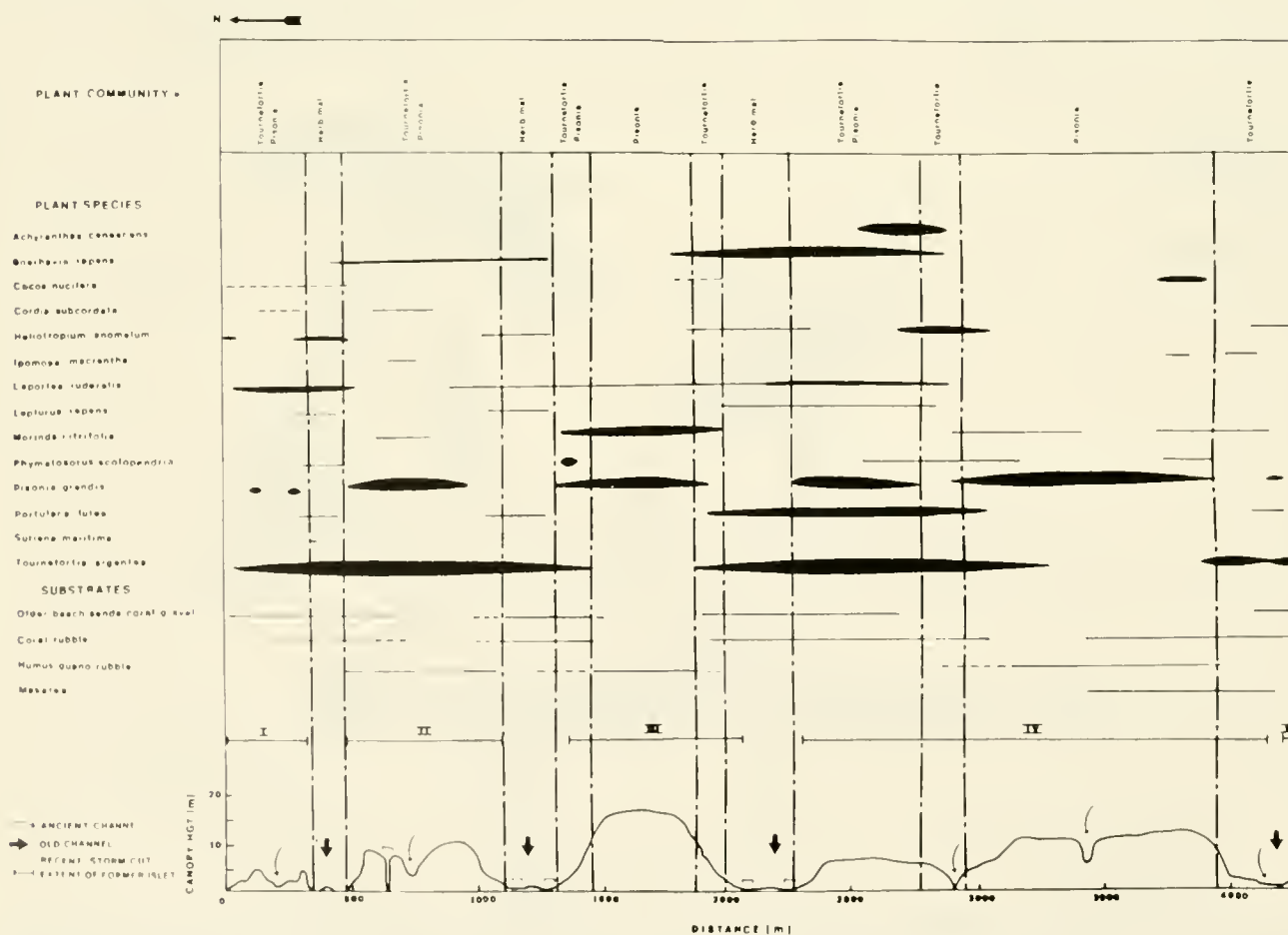


Fig. 39. Long Island: north-south transect showing division into former islets, floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated. The exact locations of the formerly more extensive *Cocos* plantations are unknown.

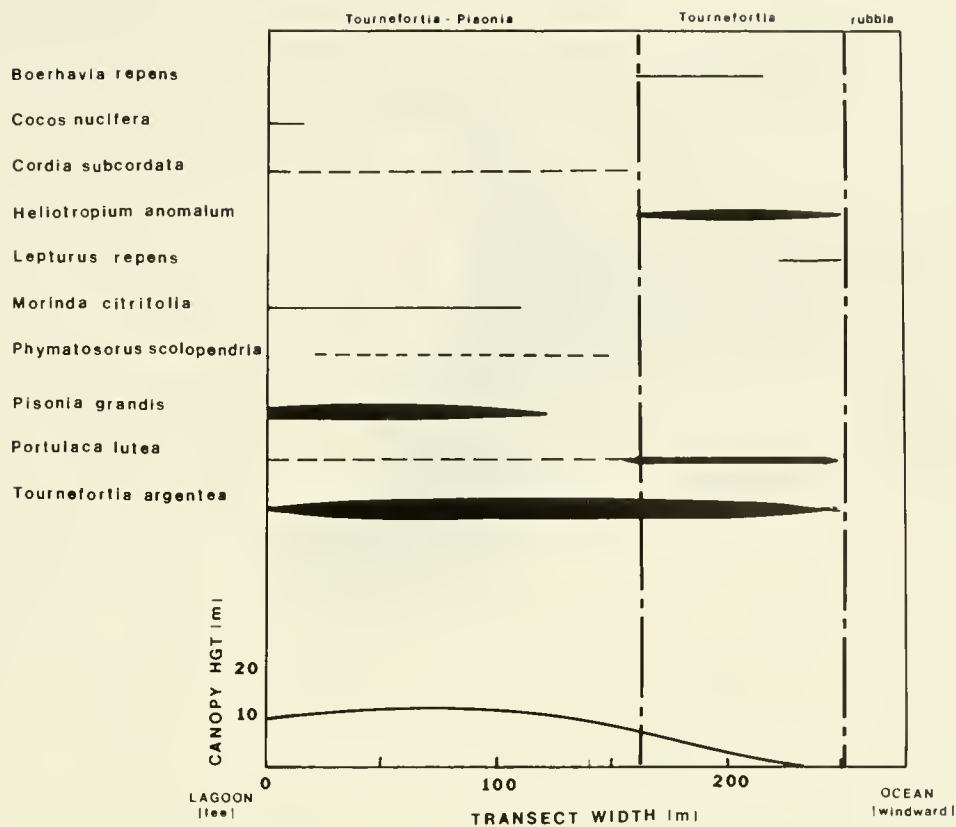


Fig. 40. Long Island: east-west cross-section through Tr. C, a former inter-islet channel, showing floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated.

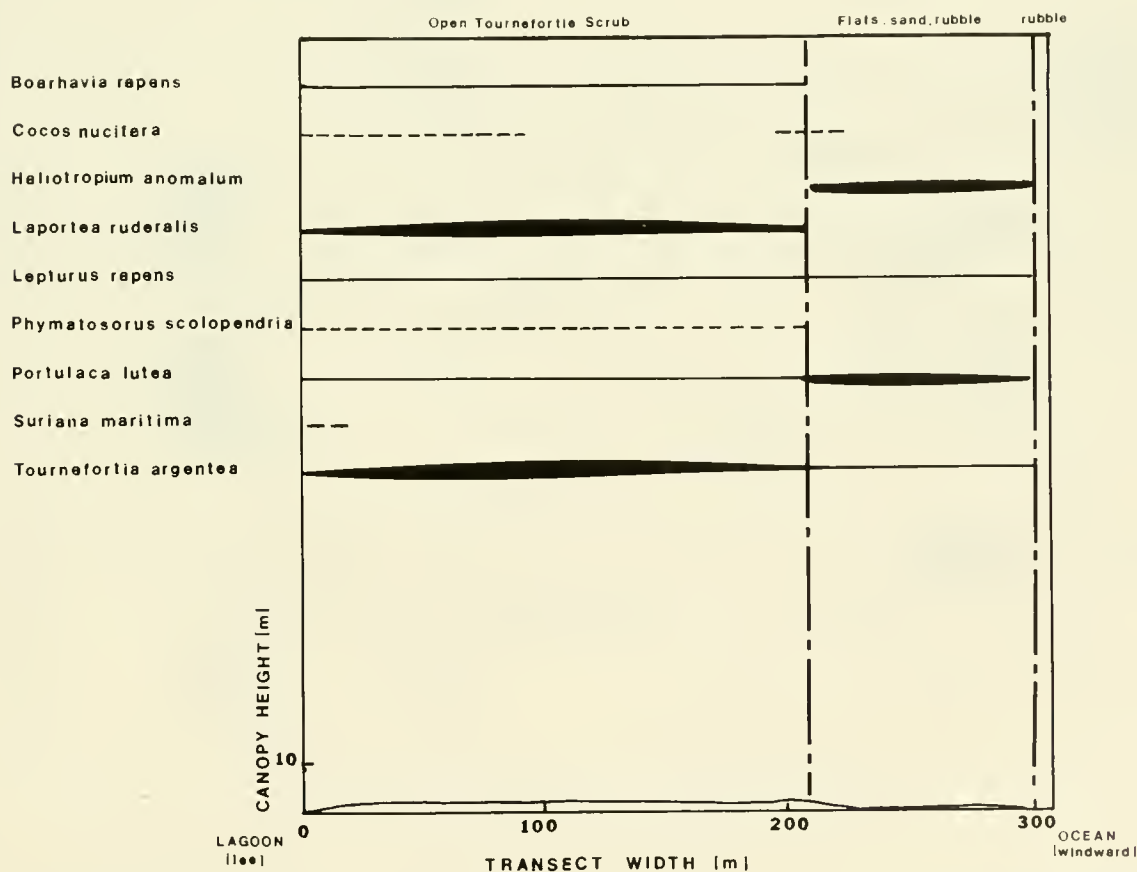


Fig. 41. Long Island: east-west cross-section through Tr. 8, which passes through mature interior *Pisonia* forest of largest of Long's coalesced motus. Data includes floristic composition, relative abundance of plant species, degree of species overlap, and canopy heights. Vertical height is exaggerated. Note the absence of low vegetation on the leeward shore.



Fig. 42. Vegetation and physiography of Windward Islet no. 1: Bo'sun Bird Islet. Scale is larger than on the vegetation maps of other islets.

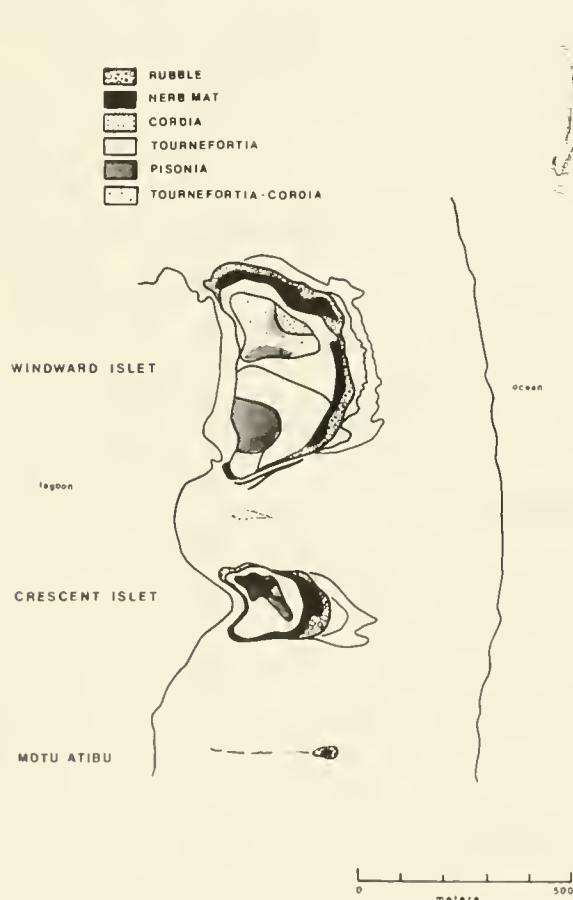


Fig. 43. Vegetation and physiography of Windward Islets nos. 2, 3 and 4: Windward and Crescent Islets, and Motu Atibu ("Coral Rubble Islet"). Atibu appears to have been severely damaged during the February 1990 storm.

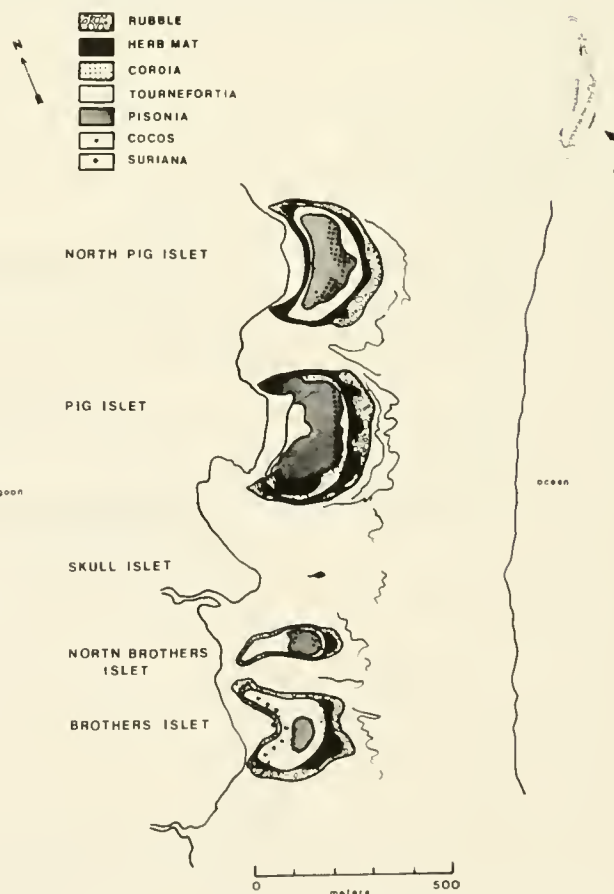


Fig. 44. Vegetation and physiography of Windward Islets nos. 5 through 9: North Pig, Pig, Skull, North Brothers, and Brothers Islets. Note the reefs extending westward into the lagoon.

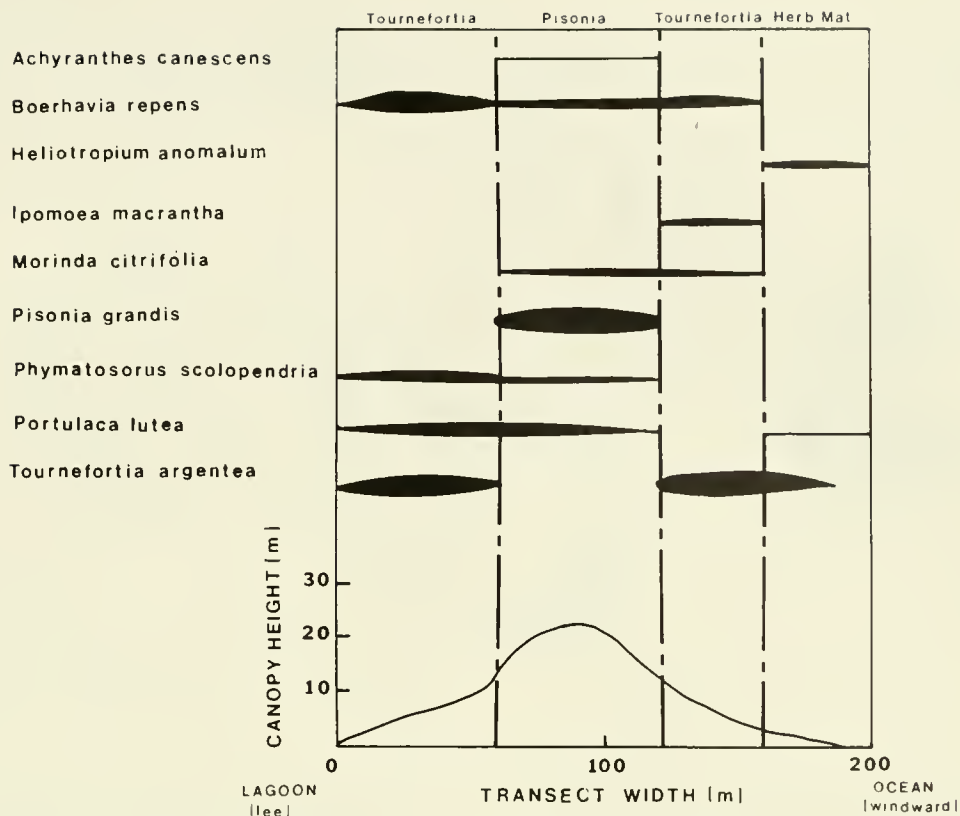


Fig. 45. Pig Islet: east-west cross-section through center of islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Pig's profile is especially symmetrical. It is remarkable that this islet was totally felled for coconuts in 1920.

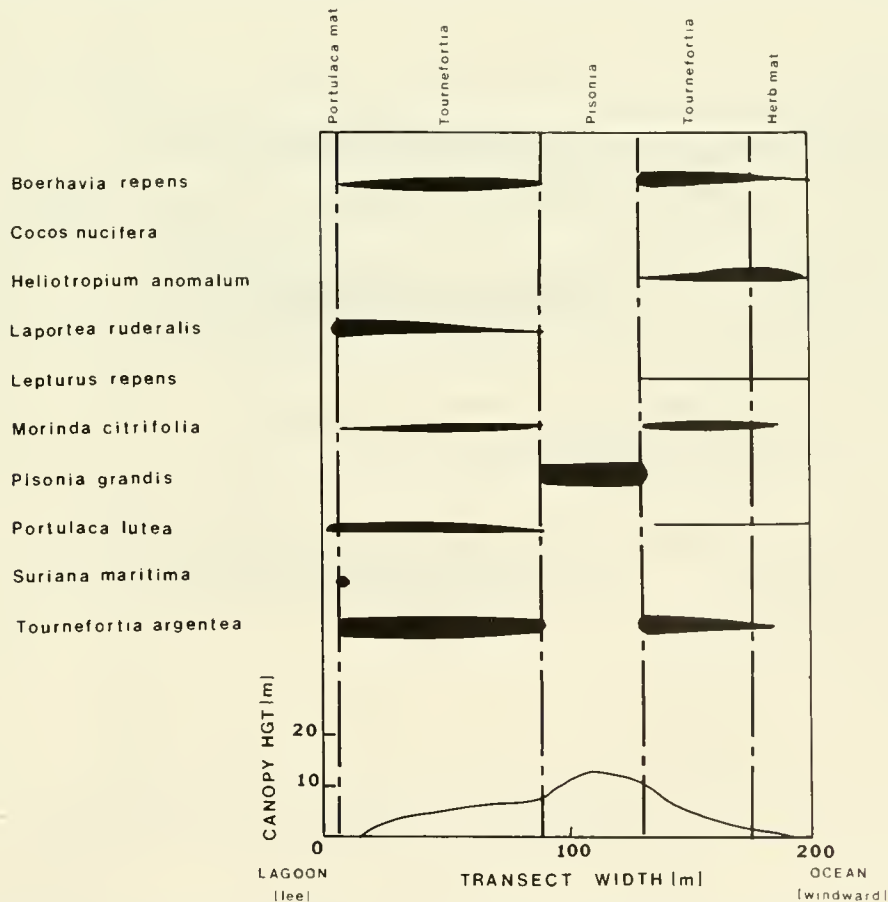


Fig. 46. Brothers Islet: east-west cross-section through center of islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Note the central monotypic stand of *Pisonia* forest. This islet's forests were totally felled in 1920.



Fig. 47. Vegetation and physiography of Windward Islets nos. 10 through 12: Noddy Rock, North Arundel, and Arundel. See text for explanation of the relatively small amount of *Pisonia* cover (Description and Ecology of the Motus Section).



Fig. 48. Vegetation and physiography of Windward Islet no. 13: Tridacna Islet. The best quality *Acropora-Tridacna* reefs extend clear across the lagoon from this motu. See Desc. and Ecol. of the Motus Section for explanation of unusual forest cover.

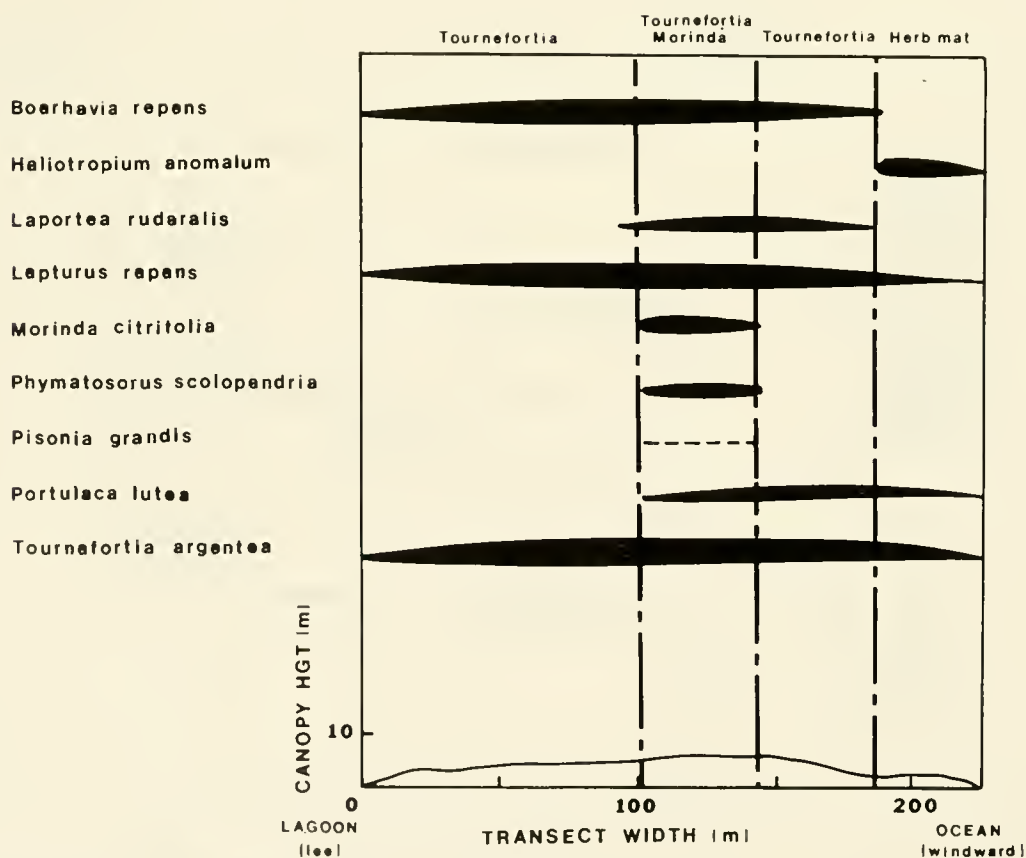


Fig. 49. Tridacna Islet. east-west cross-section through lower center of motu. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Note the absence of well-developed interior forests, unusual for a motu of this size (Description and Ecology of the Motus Section).

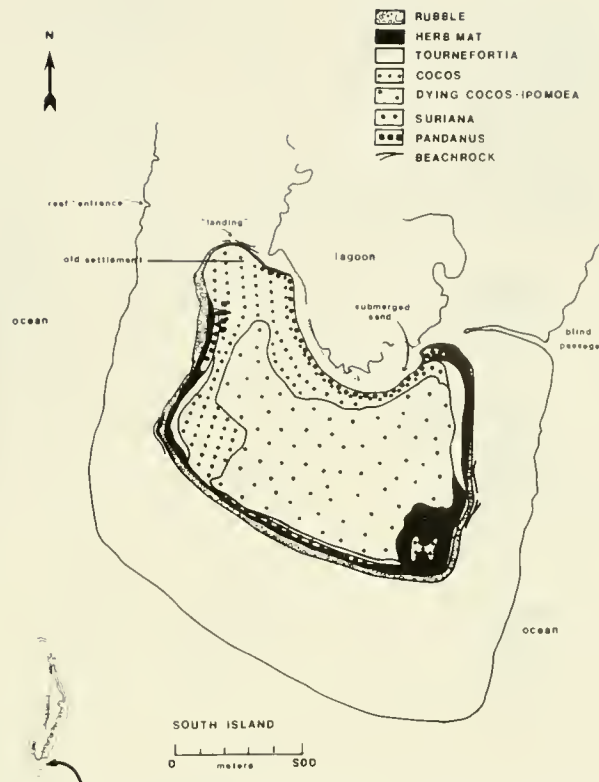


Fig. 50. South Island: vegetation and physiography. Note the accepted landing route across its leeward reef flats.

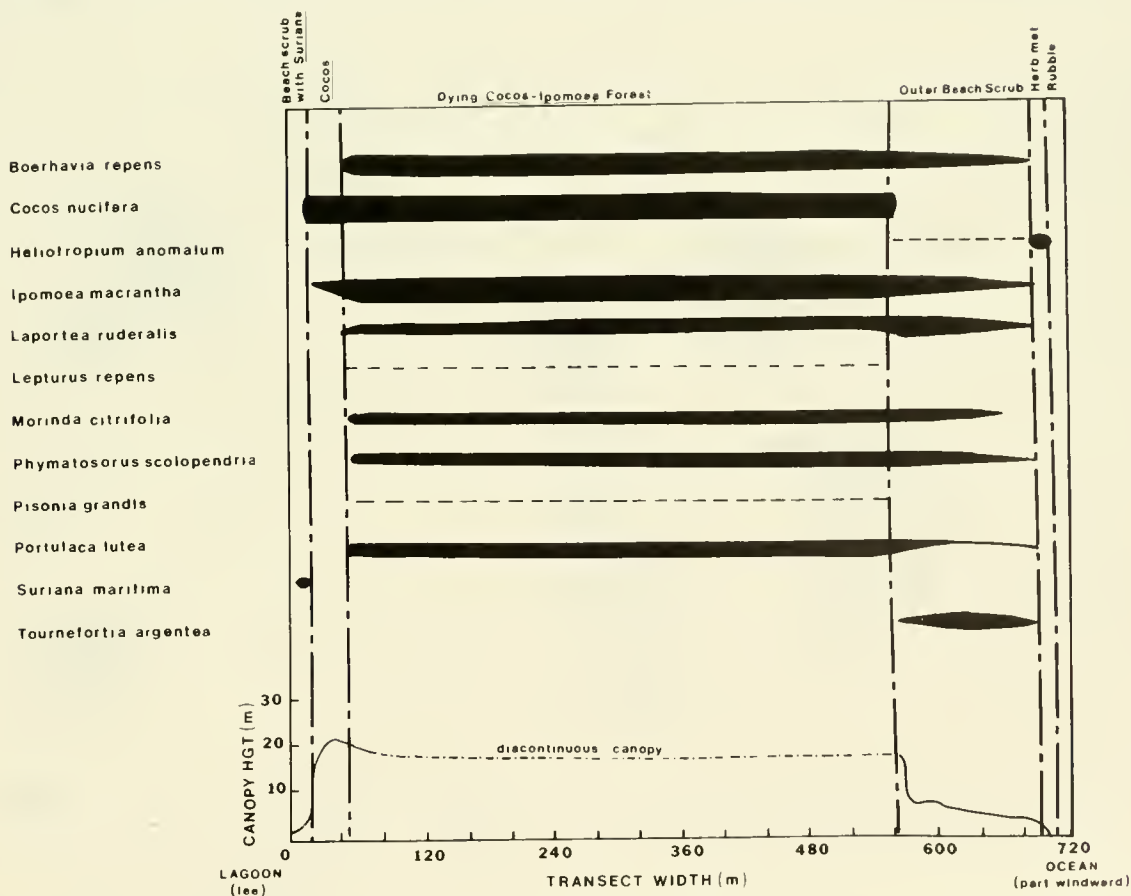


Fig. 51. South Island: distribution and abundance of plant species along Tr. 2, which runs at an angle of 60° from the lagoon to the south shore through the western center of the islet. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated. Horizontal scale is half that of the profiles from smaller motus.

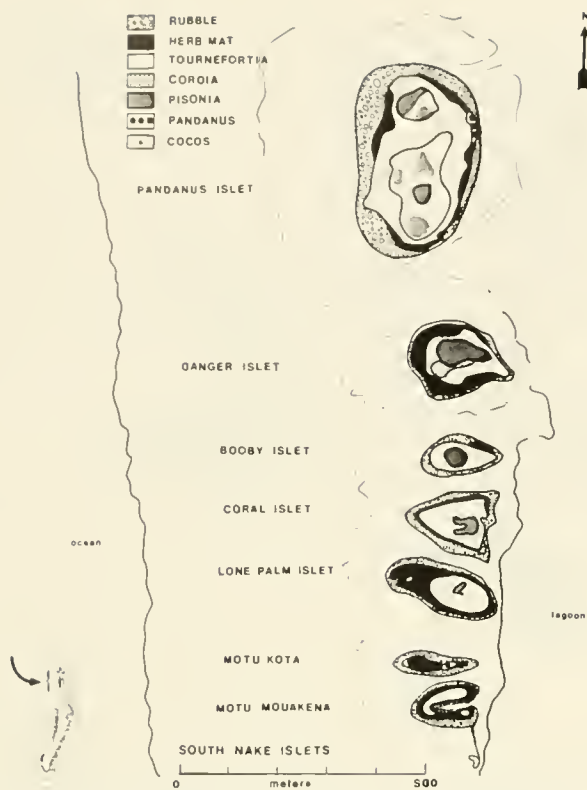


Fig. 52. Vegetation and physiography of the 7 South Nake Islets: Pandanus, Danger, Booby, Coral, and Lone Palm Islets, Motu Kota ("Red-footed Booby Islet"), and Motu Mouakena ("Masked Booby Islet").



Fig. 53. Vegetation and physiography of Central Leeward Islet no. 1: Motu Mannikiba ("Seabird Islet").

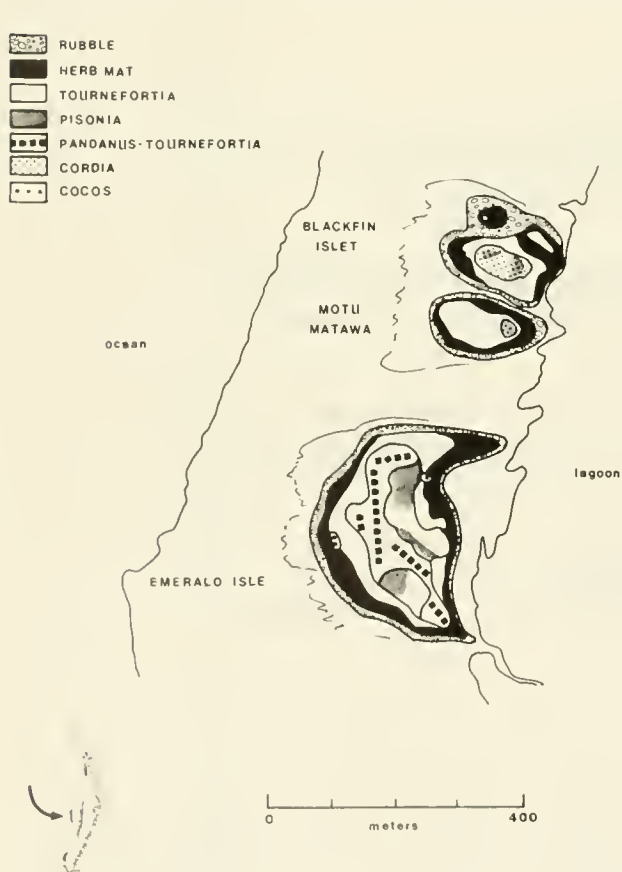


Fig. 54. Vegetation and physiography of the Central Leeward Islets nos. 2 through 4: Blackfin Islet, Motu Matawa ("Fairy Tern Islet"), and Emerald Isle.

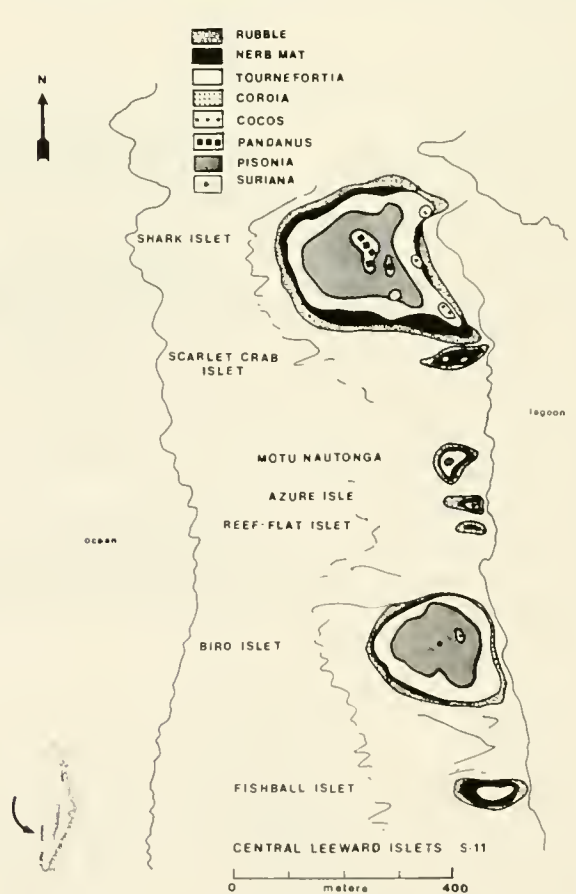


Fig. 55. Vegetation and physiography of the Central Leeward Islets nos. 5 through 11: Shark and Scarlet Crab Islets, Motu Nautonga ("Sea Cucumber Islet"), Azure Isle, Reef-flat, Bird and Fishball Islets.

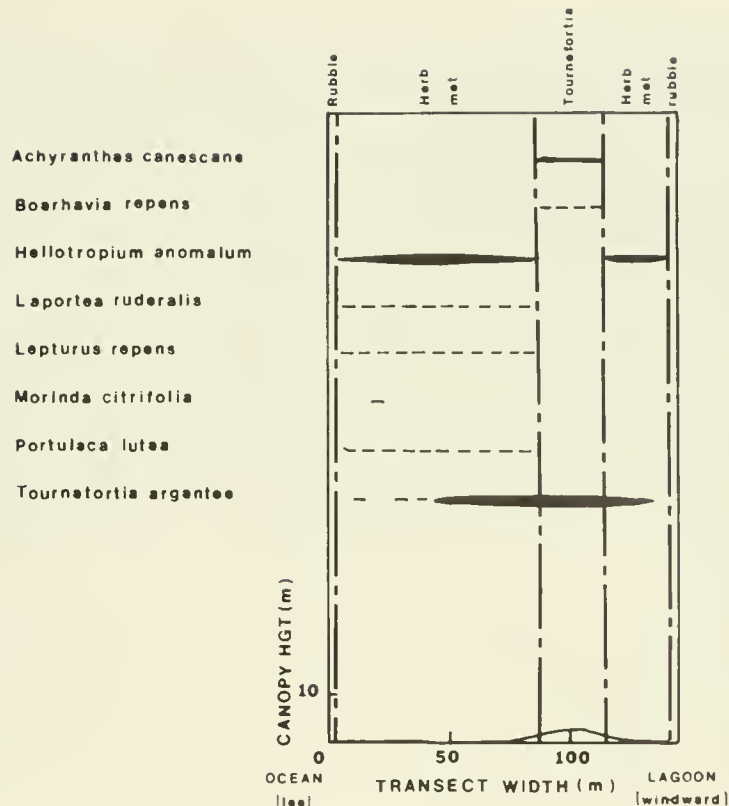


Fig. 56. Fishball Islet (no. 11, Central Leewards): east-west cross-section through the center of this young motu, which exhibits early stages of geological and biological evolution. Data includes floristic composition, relative abundance of plant species, degree of species overlap and canopy heights. Vertical height is exaggerated.

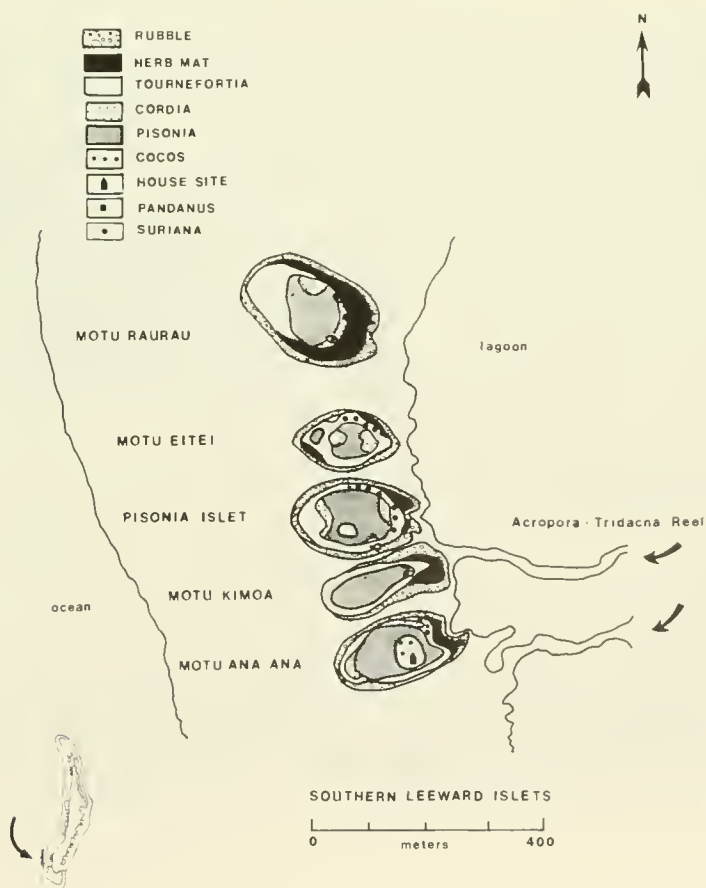


Fig. 57. Vegetation and physiography of the 5 Southern Leeward Islets: Motus Raurau ("Blue-gray Noddy Islet"), Eitei ("Frigatebird Islet"), Pisonia Islet, Kimoa ("Rat Islet"), and Ana-Ana ("Anne's Islet").



Pl. 1. A dawn view of Caroline as seen from the ocean in 1988 but virtually identical with that seen by the atoll's Western "discoverer," de Quiros, in 1606.



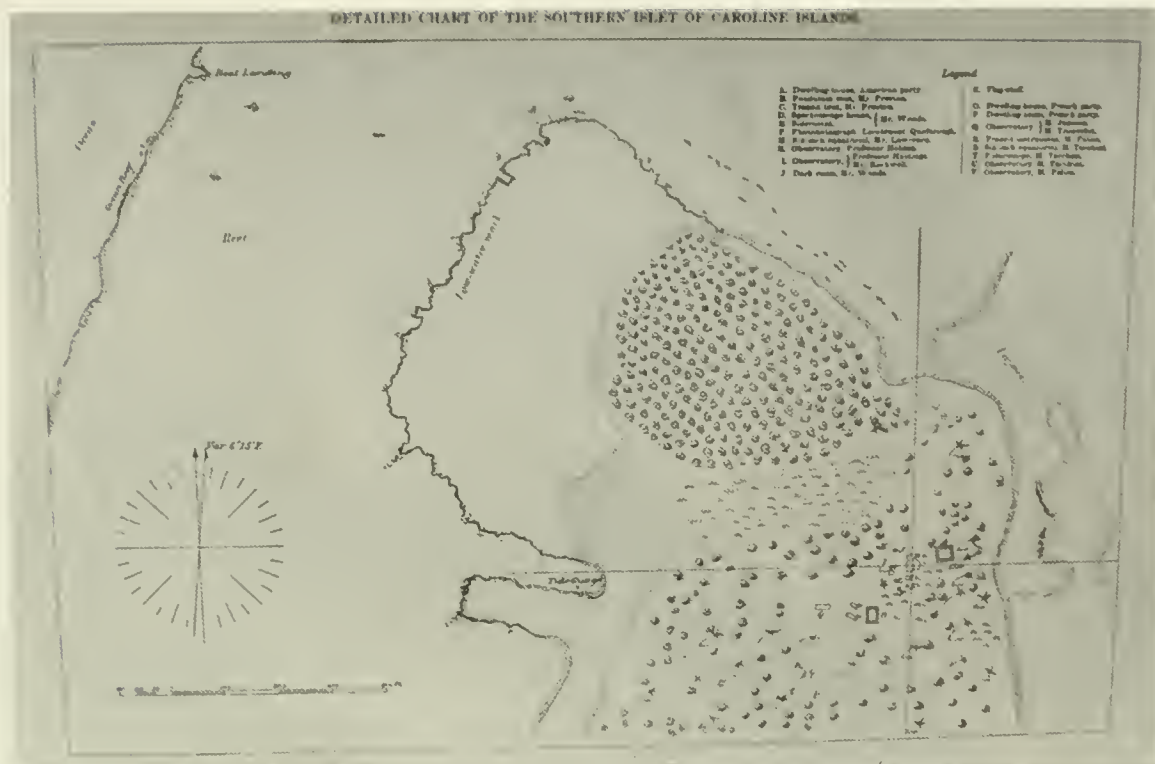
Pl. 2a. A clearing on South Island from which the Solar Eclipse Party made their observations in 1883. Today the area is covered with dense *Cocos* forest (from Holden & Qualtrough, 1884).



Pl. 2b. One of the three European-style houses that have ever been built on Caroline, drawn in 1883 (*ibid.*).



Pl. 3a. An artist's very free rendering of Caroline in 1883 (from Holden & Qualtrough, 1884).



Pl. 3b. Map of the "settlement" on South Island, as drawn by the Solar Eclipse Party (ibid.).



Pl. 4. Two lagoon views a century ago along the north coast of South Island (from Holden & Qualtrough, 1884). Compare these drawings with Plate 24.



Pl. 5a,b. Motu Ana-Ana, unnamed in 1883 (Holden & Qualtrough, 1884) but appearing virtually identical then and today (Plate 81). Below is a substantial *Tournefortia* tree along South Island's lagoon edge.



Pl. 6. Base camp, northwest peninsula, South Island.





Pl. 7. The junior author beside an entangling thicket of *Ipomoea macrantha*, dying Cocos-*Ipomoea* forest, interior South Island.

Pl. 8. "Rat City" base camp, southwest Long Island.





Pl. 9. Relocating camps with inflatable canoe. Cameron Kepler and Katino Teeb'aki, Bo'sun Bird Islet.



Pl. 10. Black-tipped reef shark (*Carcharhinus melanopterus*), a numerous and aggressive denizen of Caroline's lagoon. Note the abundant sea cucumbers (*Ludwigothuria* sp.).



Pl. 11. Jagged, upraised reef (*feo* or *champignon*), leeward reef, southwest Nake Island. Note the wide reef flats.



Pl. 12. Floating a small boat across the southwest reef flats in calm weather from the "boat entrance" to the "landing" on South Island. Note the wide reef flats. The *Akademik Korolev* drifts offshore.



Pl. 13. Beach crest, sandy rubble, seaward moat, and narrow reef flats off northeast Long Island.



Pl. 14. Extensive lagoon reef flats south of Arundel Island on the windward side. Note the five southern leeward islets in the distance.



Pl. 15. An incipient motu, barely connected to Motu Mouakena's southern shore. See also Fig. 69.



Pl. 16. Windward reef and peaked beach crest on South Island, with the recently wrecked remains of a 26-foot sloop.



Pl. 17. Successive ridges of coral rubble forming extensive gravel flats, northeast Nake Island.



Pl. 18. Channel between the two northern islets, Long and Nake. Note the mixed forest with *Cocos* and *Pandanus*.



Pl. 19. Noddy Rock (0.02 ha), an emergent reef platform along the windward reef flats. A northward view.



Pl. 20. Windward beach, Long Island, showing wide rubble flats inland of the beach crest, rimmed by oceanic flotsam and jetsam.



Pl. 21. Beachrock, west shore, South Island. Russian vessel *Akademik Korolev* drifts offshore and a lone *Suriana maritima* dots the blinding coral beach.



Pl. 22. A large coconut crab (*Birgus latro*) shelters in a subterranean cavity in the feo.



Pl. 23. Sandy Inlet, a filled-in portion of the lagoon, extends its fishhook-shaped mudflat 300 m northward into Nake's landmass. Here grow the healthiest and most productive *Cocos* on Caroline. Note the bristle-thighed curlews in the foreground.



Pl. 24. South Island's pure *Cocos* plantation, looking west along the lagoon. This extensive grove has now obliterated all traces of the former "settlement" (Plates 2-5).



Pl. 25. Brilliantly-colored, crystalline lagoon waters adjacent to Emerald Isle (Central Leeward Islets) are studded with twisted reef configurations and sandy channels.



Pl. 26. An impressive cross-lagoon reef of *Acropora* sp. coral and *Tridacna maxima* clam shells joins Tridacna Islet with Motu Kimoa.



Pl. 27. *Cordia* forest (to 12.6 m tall), Pig Islet.

Pl. 28. Sand, silt, rubble, and hardpan mingle on the upper reaches of Long Island adjacent to the lagoon.





Pl. 29. Caroline's best sandy beach lines the lagoon shore of Shark Islet. The fine sand is overlain with sparkling pink granules.



Pl. 30. Sheltered bay, Brothers Islet. Raurau Islet lies across the lagoon. Note the sparse herb mat and silty shallow waters.



Pl. 31. Narrow lagoon beach lined with *Tournefortia* scrub, Blackfin Islet (Central Leewards).



Pl. 32. Recent sand additions to South Island's northeast point, which is in part covered with excellent natural herb mats and healthy *Suriana* scrub (right).



Pl. 33. An old interislet channel (Transect C, Long Island), now filling in with herbs, *Tournefortia* scrub, and *Cocos*. Note the nesting masked boobies in middle right.



Pl. 34. A large clearing within dying *Cocos-Ipomoea* forest, interior South Island. Note the prolific mats of *Boerhavia* interlaced with *Phymatosorus* and *Ipomoea*.



Pl. 35. *Pandanus* forest, south Nake.

Pl. 36. An end wall of the ancient Tuomotuan *marae*, northwest Nake.





Pl. 37. Mixed forest with *Cocos*, southwest Nake Island.



Pl. 38. Orange, scarlet, and green phalanges of *Pandanus* rest on a clump of *Portulaca*. The ubiquitous *Coenobita perlatus* forage on their stringy flesh.



Pl. 39. Inner edge of lagoon, South Island, 1988. *Cocos* is progressively shading out the beach scrub with *Suriana maritima*.



Pl. 40. Inner edge of lagoon, South Island, 1965, taken from approximately the same location as Plate 39. Note the greater extent of sand and *Suriana* coverage above high water than today, due to less encroachment and shading by the palms.



Pl. 41. Heavy understory of *Achyranthes canescens*, *Boerhavia repens*, and *Phymatosorus scolopendria* in a clearing adjacent to *Pisonia* forest, Pig Islet.



Pl. 42. *Boerhavia* fruits on feathers and bill of a great frigatebird.



Pl. 43. Inside a mature *Pisonia grandis* forest, interior Nake Island. Note the barren, dark aspect, virtually devoid of undergrowth except root suckers.



Pl. 44. Fringe of *Suriana*, northeast point, South Island.



Pl. 45. Well developed natural herb mat, primarily *Heliotropium anomalum* and *Lepturus repens*. Scattered *Tournefortia* form a "savannah." Here the sandy soils are conducive to the growth of lush *Heliotropium*, northeast point, South Island.



Pl. 46. Detail of *Heliotropium anomalum*, with remains of the first evidence of tropicbirds on Caroline, Skull Islet.



Pl. 47. *Tournefortia* scrub, fringed by a natural herb mat, and occupied by a colony of sooty terns. An old interislet channel, northern Long Island. Note the nesting red-footed boobies.



Pl. 48. *Tournefortia*-*Morinda* forest, with nesting brown noddies, interior Tridacna Islet.



Pl. 49. Skull Islet (0.02 ha), with brown noddie terns, looking east to the windward reef.



Pl. 50. An artistic impression of a *Pandanus* grove, South Island, in 1883 (from Holden & Qualtrough, 1884).



Pl. 51. Red-footed booby in *Tournefortia* scrub, Motu Raurau.



Pl. 52. Mature *Pisonia grandis* canopy with incubating black noddies and a white tern, Pig Islet. With a canopy height of 21 m, this was the most majestic interior forest on the atoll, although it cannot be older than 65 years.



Pl. 53. Azure Isle (Central Leewards)—an example of a motu containing a single *Pisonia* tree. Note the narrow, but still shark-patrolled, interislet channel. View east from Motu Nautonga, with Brothers Islet in the distance.



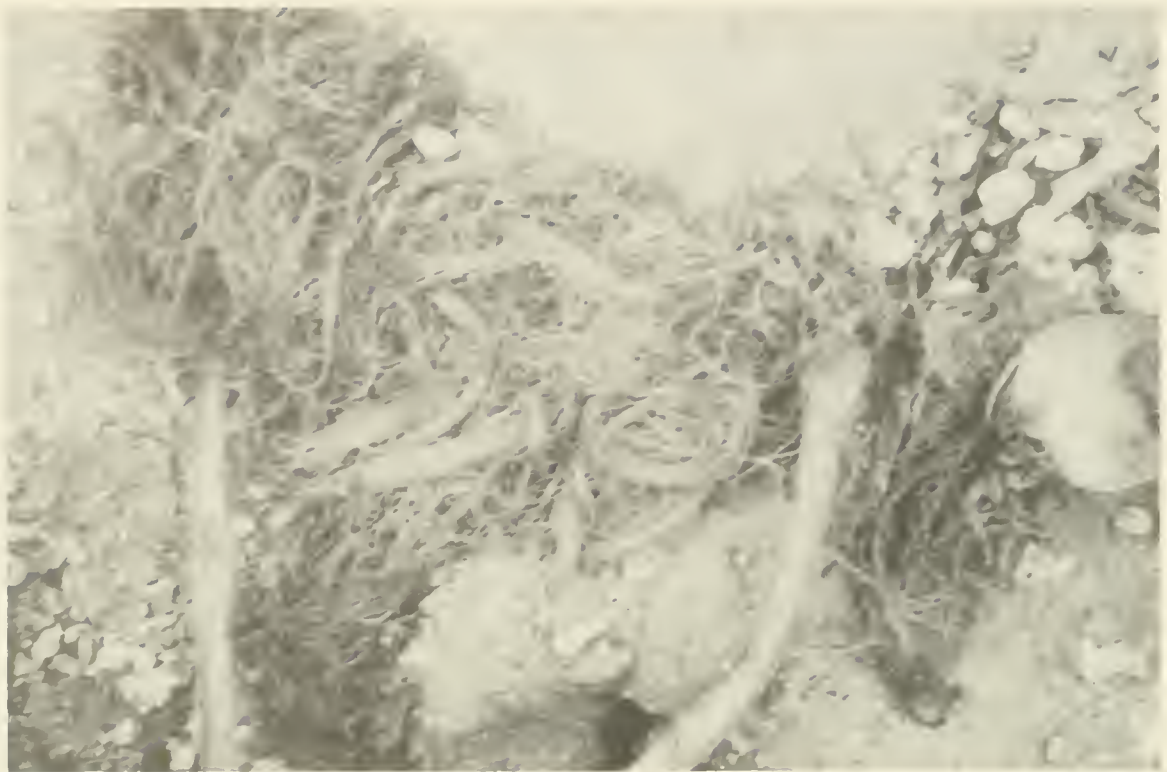
Pl. 54. Caroline's sole clearing, with Tahitian-style huts, Motu Ana-Ana.



Pl. 55. White tern "nest" balances precariously on the upper midrib of a coconut frond.



Pl. 56. Average-sized coconut crab (*Birgus latro*) on Caroline. Compare its size with the coconut.



Pl. 57. Piles of fibrous shavings—coconut crab sign.



Pl. 58. Beachrock at the lower end of Long Island, typically found at low water.



Pl. 59. Sooty terns (Colony A)—approximately 128,000 pairs occupy a scrubby swath of vegetation in the north-central portion of Long Island, the location of an old interislet channel. Note *Cocos* on the right and a mound of *Pisonia* at rear.



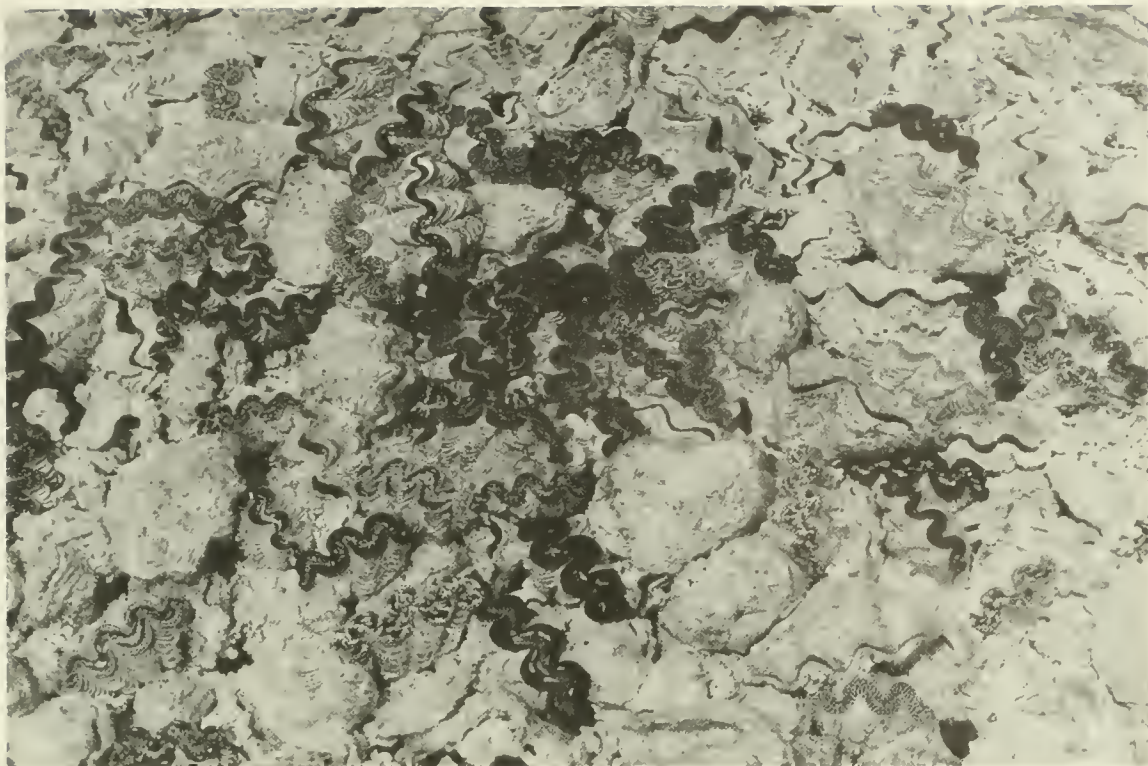
Pl. 60. Windward Islets numbers 5–9 (left to right): North Pig, Pig, Skull (not visible), North Brothers, and Brothers.



Pl. 61. North Pig (left) and Pig (right) Islets: a southeasterly view across the coral-studded lagoon from Shark Islet. Note the expansive, central *Pisonia* forests.



Pl. 62. Arundel Islet (foreground), looking south-southwest across Tridaena Islet to South Island. Distant Motu Ana-Ana lies on the right.



Pl. 63. Detail, *Tridacna maxima* reefs, lagoonside of Tridacna Islet. This dense aggregation of giant clams amassed up to 80 per square meter.



Pl. 64. View of Pandanus Islet (center) west down the channel separating Nake (right) and Long (left) Islands.



Pl. 65. Danger Islet (South Nake number 2), looking due west across the shallow upper lagoon from Long Island.



Pl. 66. South Nake Islets numbers 3-6 (right to left): Booby, Coral, Lone Palm, and Kota. Westerly view across the shallow upper lagoon from Long Island.



Pl. 67. Lone Palm Islet (South Nake number 5): a southerly view from the shallow tidal flats of Coral Islet. Plate 68 provides a more detailed view of the lower part of the chain.



Pl. 68. South Nake Islets numbers 2–6 (right to left): Danger, Booby, Coral, Lone Palm, and Kota, from a boat. This view shows better detail of the lower part of the chain than Plate 67.



Pl. 69. Motu Mouakena (South Nake number 7), with its sandy cay. A westerly view from the upper lagoon. Compare with Plate 15.



Pl. 70. North end, Motu Mannikiba "Seabird Islet" (Central Leewards number 1), showing mounds of *Pisonia* and a closer *Cocos* grove. Note coral "mushroom" in lagoon.



Pl. 71. Motu Mannikiba, looking west along Transect 1. Natural herb mats on coral rubble give way to *Tournefortia*, then a distant patch of *Pisonia*.



Pl. 72. Motu Mannikiba, looking west along Transect 2. Low *Tournefortia* scrub covers a coarse, rubbly substrate which was probably once an inter-slet channel.



Pl. 73. Blackfin Islet (Central Leewards number 2) lies to the left of the ship. View west-southwest from the tip of Long Island.



Pl. 74. A stunning "blue hole" within the lagoon off the southwest point of Emerald Isle (Central Leewards number 4).



Pl. 75. Mixed *Pandanus*-*Tournefortia* forest, interior Emerald Isle.

Pl. 76. Emerald Isle, looking west across hardpan and open lagoonside scrub to a densely vegetated interior.





Pl. 77. Shark Islet (Central Leewards number 5): view across crystalline shallow waters to Caroline's sole sandy beach.



Pl. 78. Southern Leeward Islets numbers 1-5 (right to left): motus Raurau and Eitei, Pisonia Islet, motus Kimoa and Ana-Ana. View northwest from Tridaena Islet.



Pl. 79. View of Motu Raurau ("Blue-gray Noddy Islet") from Motu Eitei ("Frigatebird Islet"). Note the two nutrient-starved, chlorotic *Cordia* trees growing in almost pure rubble (center left).



Pl. 80. View of Motu Kimoa ("Rat Islet") from Pisonia Islet. Its central forest, typical of the Southern Leewards, is a mixture of *Pisonia* and *Cordia*.



Pl. 81. Motu Ana-Ana ("Anne's Islet"): a view with giant ray, from the shallows of the lagoon's southern end adjacent to South Island. Note the similarity to Plate 5, dating from 1883.

Appendix 1

Reef Information for Navigators

We include this section because no accurate hydrological chart exists, and the *Pacific Islands Pilot* (Hydrographer of the Navy, 1982) section for Caroline is incomplete. Arundel's 1883 map (Admiralty Chart No. 979, Fig. 4) is still used today.

Caroline has neither a deep pass, nor navigable channels into the lagoon, nor a ship anchorage beyond the reef. In 1873, a set of moorings was placed off the west coast of South Island for the convenience of guano ships, approximately "a mile north of the south-west point, in about 60 fathoms of water and some distance from the shore" (Maude, ca. 1942). These are long gone, although small boats can still anchor within the close lee of South Island during normal trade winds. Today's ships, however, must drift well offshore after approaching the atoll from the west (Pl. 12).

Of special note is a possible extension of the perimeter reef south and southwest of Caroline. Arundel's map notes: "Reef reported to extend four cables from southeast point." This information probably originated in Findlay's *South Pacific Directory* of 1884, quoted by Holden (1884). Evidently the windward reef of South Island extends approximately 1.7 km from its southeast point. From here "this reef sends out two branches to a distance of 2.5 km, one toward the southeast, the other toward the southwest and is consequently dangerous to approach at night." Arundel's map does not include this bifurcation which, according to Findlay (1884), extends at least across the width of South Island. He also states that "a landing (not always safe) may be effected on the north side of the southwest bifurcation, described above." No trace of these submerged reefs is evident on the RNZAF aerial photos.

The "boat entrance" (Fig. 4), a narrow nick in the outer leeward reef, marked by the stock and ring of an anchor and immediately to the west of South Island's northwest point, is not necessarily the easiest route to the lagoon. Landing is possible across the steep-to reef at many locations along the leeward reef; opposite the southern end of Ana-Ana is good.

Landing is fairly straightforward by the anchor when the seas are calm, especially when one becomes familiar with the crooked notch that narrowly pierces the outer reef. After negotiating a powerful backwash, one's boat is swept onto the shallow reef flats—liberally laced with chunks of jagged reef—which is exposed at low tide and barely covered at high tide. A swift current passes west out of the lagoon between South Island and Ana-Ana, sweeping over the reef at the notch. Only small craft with virtually no draft can effect the 500-m journey to South Island. Because the shallows are unchanneled and not navigable even at high tide, one's small boat must be carefully hauled through the water to a sheltered landing spot adjacent to South Island's northwest point (Pl. 12).

An alternative landing method used by yachts in calm weather is via the "blind passage" (Structure and Topography section, Fig. 50), adjacent to the northeast corner of South Island. Despite the fact that the inner one-third of this narrow diverticulum is calm (and used for the residents' yacht mooring), the outer two-thirds are rough and dangerous most of the time. Its channel leading to and from the open sea is particularly turbulent and should not be attempted without assistance from the residents, and only at first light.

Appendix 2

Weather Data, Caroline Atoll, 1989-1990

A. Wind Direction and Speed (mph), 1989

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	NNE 15	NW 18	E 25	E 12	E 20	E 15	E 25	E 20	-	NE 10	N 20	NE 8
2	NE 10	W 5	E 15	E 16	E 20	NE 18	SE 20	E 12	-	NE 12	N 15-17	NE 10
		Variable										
3	NE 10	NE 20	E 12	SE 14	S 15-20	E 18	E 20	SE 25	-	NE 15	NE 15	NW 20
4	NE 15	NE 15	E 12	SE 15	E 15	E 15	E 20	SE 20	-	NE 15	NE 12	NW 20
5	NE 20	NE 15	NE 15	E 12	NE 8	E 15	E 18	E 18	-	NE 12	E 12 big swells	NW 18
6	NE 20	NE 20		SE 10	NE 8	E 15	E 10	E 18	-	NE 12	E 10	N 10
7	NE 12	SE 18	E 12	E 14	NE 10	NE 25	-	E 12	-	NE 15	NE 12	NW 18
					E 10							
8	NE 12	E 15	calm	SE 10	E 10	NE 20	SE 12 squalls	NE 18	-	NE 15	calm	NW 18
9	NE 12	E 18	SE 10	E 20	E 15	NE 18	SE 20	E 12	-	NE 12	N 10	NE 10
10	NE 15	E 16	NW 10	E 20	E 15	E 15	SE 16	E 12	-	NE 10	NE 12	NE 10
11	NE 10	NE 16	calm	SE 25- E 10 squalls	E 15	NE 15- E 15	E 15	calm	-	NE 10	E 18	NE 5
12	NE 20	SE 14	E 10	W 14	E 15	E 15	E 12	E 12	-	NE 16	E 17	NE 12
13	NE 15	E 12	E 12	E 16	NE 16	NE 16	E 12	-	-	NE 11	E 14	NE 12
14	NE 15	E 10	NE 10-18	E 20	NE 16	NE 8	E 12	calm	-	ENE 10	E 10	NE 14
15	NE 15	NE 8	E 8	E 18	E 15	E 10	E 10	-	-	NE 10	calm	NE 14
16	NE 15	SE 8	E 12	E 18	E 22 squalls	E 10	NE 10	-	-	NE 12	calm	NE 15
17	NE 18	E 20	NE 15	E 18	E 25	E 15	E 10	-	-	NE 14	calm	NE 12
18	NE 12	E 12	E 8	E 18	NE 18	E 15 big swells	E 15	-	-	NE 15	N	NE 14
19	NE 12	E 12	E 10	E 18	NE 14	E 10	E 16	-	-	NE 13	NW 10	E 12
20	NE 18	E 12	E 10	E 18	NE 14	E 15	E 18	-	-	E 15	NW 15	E 10
21	NE 15	NE 10	SE 8	E 14	E 12	NE 20	E 20 squalls	-	-	E 16	N 16	E 10 big swells
22	NE 20	E 15	calm	E 14	E 12	E 10	E 15	-	-	NE 14	NE 14	E 12-NE 10
23	NE 18	thunder squalls	N 18	SE 14	SE 10	E 10	E 15	-	NE 20-30	E 20	NE 16	calm
24	NE 15	E 25	N 12	SE 14	SE 10-25	E 10	E 12	-	E 20-30	NE 15	NE 12	NE 15
25	NE 12	E 15	N 12	E 12	E 18	SE 17	E 10	-	E 20	NE 15	NE 12	NE 16
26	NE 12	E 15	N 10	E 10	NE 14	E 10	calm	-	E 20	NE 15	N 10	NE 15
27	NE 12	E 25	SE 10	NE 10	E 18	E 10	calm	-	NE 17	E 9	E 9	NE 15
28	NE 12	E 14	E 12	E 13	E 18	E 10	E 15-35	-	E 15	NE 10	E 8	NE 15
29	NE 15		E 14	E 18 big swells	E 15	E 18	E 15	-	N 10	NE 8	E 7	NE 12
30	NE 12		E 12	E 13	-	E 18	E 15	-	calm	calm	-	E 10
31	calm		E 18				SE 18	-		N 20		E 16

B. Rainfall, 1989–1990

Month/Year	Mean Monthly Rainfall (mm)	Mean Number of Rain Days
Jan '89	71.1	7
'90	177.8	22
Feb '89	160.0	14
'90	640.1	10
Mar '89	259.1	20
'90	215.9	14
Apr '89	190.5	16
'90	48.3	6
May '89	66.0	10
'90	325.1	8
Jun '89	48.3	11
'90	78.7	11
Jul '89	45.7	12
'90	68.6	8
Aug '89	35.6	12 ^a
'90	109.2	14
Sep '89	50.8	3 ^b
'90	81.3	6
Oct '89	73.7	11
'90	175.3	9 ^c
Nov '89	78.7	7
'90	134.6	14
Dec '89	162.6	11
'90	154.9	9
Annual '89	1,242.1	134
'90	2,209.8	131

Source: Ron Falconer, Caroline Atoll (personal communication).

^aBased on 16 days' data.

^bBased on 9 days' data.

^cBased on 18 days' data.

1.2 Ecological Studies on Caroline Atoll, Republic of Kiribati, South-central Pacific Ocean

Part 2. Seabirds, Other Terrestrial Animals, and Conservation

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Introduction

On 26 July 1988, the Soviet research vessel *Akademik Korolev* sailed from Vladivostok enroute to Dutch Harbor, Alaska. There, Soviet oceanographers joined their American colleagues to investigate the Gulf of Alaska and the Chukchi Sea in the Third Joint US–USSR Bering & Chukchi Seas Expedition. When the arctic research was completed in early September, the ship headed toward the central Pacific. A rendezvous for a second contingent of Americans took place in Hilo, Hawaii, on 9 September. Six Americans joined the ship, which set sail on a cruise track of 14,892 km that terminated 6 weeks later in Singapore. An important part of the expedition was research in and around little-known Caroline Atoll, at the southeastern edge of the Line Group. On Christmas Island, we picked up Katino Teeb'aki, a conservation officer for the Republic of Kiribati, who represented his government and helped our land-based research efforts. After landing on Caroline on 22 September, we camped in 2 locations for 7 nights, surveying the terrestrial plants and animals on all 39 islets. Caroline is a remarkably pristine atoll with its native plant communities nearly intact on all but three islets, and teeming seabird communities that, collectively, are second in the Line Group only to Christmas Island (Kiribati) in diversity. For several historical reasons, the natural values of this spectacular blend of marine and terrestrial resources have been overlooked.

Approximately 1,000,000 seabirds of 11 species bred on Caroline Atoll in November 1988. The most abundant species, with over 900,000 birds in 1988, was the sooty tern (*Sterna fuscata*). Two species (red-tailed tropicbird [*Phaethon rubricauda*], blue-gray noddy [*Procelsterna cerulea*]) are reported breeding for the first time. The known seabird fauna now includes one tropicbird, three boobies, two frigatebirds, and five terns.

Seabird distribution on Caroline is determined by the distribution of plant communities, rats, coconut crabs (*Birgus latro*), and the prevailing trade winds. Red-tailed tropicbirds and ground-nesting brown noddies (*Anous stolidus*) nested on small islets relatively free of rats and coconut crabs. masked and brown boobies (*Sula leucogaster*) preferred exposed windward beaches, primarily on Long and Nike. The tree-nesting red-footed booby (*Sula sula*) and the frigatebirds

attained their highest nest densities in areas with reduced wind speed. The black noddy (*Anous minutus*) was found in dense colonies, generally high in *Pisonia* trees in the center of small islets, while the uncommon blue-gray noddy (*Procelsterna cerulea*) nested solitarily on open coral rubble. Sooty terns nested in large colonies, generally near or under relatively open *Tournefortia* scrub but also in open areas under *Tournefortia* and closed-canopy *Pisonia* forests. Tree-nesting brown noddies and white terns (*Gygis alba*) were found throughout the native forests and were the only species that nested in anthropogenic forests. Disturbed forests on South and Nike held the lowest seabird population densities, and no birds nested on inhabited Motu Ana-Ana.

About 300 bristle-thighed curlews (*Numenius tahitiensis*), a rare shorebird, overwinter on Caroline, foraging in all terrestrial habitats, including *Pisonia* and *Cocos–Ipomoea* forests. We extended the known winter range of the long-tailed cuckoo by discovering a small population on the atoll, the first record for the Southern Line Islands.

The known lizard fauna was increased from three to six species. Approximately 2,200 coconut crabs inhabited 12 islets on Caroline. Although primarily associated with coconut plantations, we also found them in *Pisonia* and *Tournefortia*.

We now know that the populations of seabirds and coconut crabs on Caroline Atoll are of national and international importance. The black noddy (17,000 birds) and white tern (8,000 birds) populations are the largest in the Republic of Kiribati, while the red-footed booby population (7,000 birds) is the fifth largest in the world.

History of Ornithological Studies

“There were a great quantity of sea birds of several kinds, and so importunate that they seemed to want to attack the men” (Markham, 1904). So wrote the Portuguese explorer de Quiros on 21 February 1601, the first European to see Caroline Atoll.

Precisely what seabirds were present remained a mystery until the island was surveyed 364 years later by the Pacific Ocean Biological Survey Program (POBSP) (Clapp & Sibley, 1971a). Prior to this expedition, accounts of the avifauna had been incomplete and somewhat confused. Bennett (1840) described red-footed boobies, a frigatebird (species ?), white

terns, bristle-thighed curlews, tattlers (*Heteroscelus incanum* and *H. brevipes*), and “a great number of small pigeons” with white heads (certainly noddies, perhaps both *A. minutus* and *A. stoloides*). The “shoal birds” that greeted him were probably sooty terns. His most unusual contribution was mention of a possible flightless rail: “The other birds of the coast were a kind resembling a coot...” (p. 372).

The 1883 Solar Eclipse Party (Subchapter 1.1, History of Caroline Atoll section) published a few sketchy notes, adding lesser golden-plover (*Pluvialis dominica*), reef heron (*Egretta sacra*), and masked booby (*Sula dactylatra*) (“gannet”) to the bird list. Of dubious identity were two species of “seagull” and a “snipe” (Dixon, 1884). Holden, one of the astronomers, heard “the notes of a singing bird,” which prompted us to add mist nets to our equipment in the hopes of capturing an *Acrocephalus* warbler. This resulted in our discovery of the long-tailed cuckoo (*Eudynamis taitensis*) (Ellis *et al.*, 1990) and piqued our curiosity about what Holden might really have heard.

The POBSP expedition spent 3 days on Caroline in June 1965. They found 10 species of seabirds (9 breeders), 4 migrant shorebirds, and a reef heron (Clapp & Sibley, 1971a), providing rough population estimates for each species. This work laid the foundation for later expeditions. Brief visits to Caroline by the Kiribati government in 1974 and Roger Perry in 1977 (Garnett, 1983) added no further information.

The 1988 expedition to Caroline was longer and more extensive than all former visits. We found three new island records: a breeding seabird (red-tailed tropicbird), a shorebird (Sanderling [*Crocethia alba*]), and a migratory land bird (long-tailed cuckoo), and determined islet-by-islet distributions for each species. Our population estimates, calculated from field work, aerial photographs, and detailed vegetation analysis, indicate that Caroline’s avifauna is far more important than had previously been suspected (King, 1973; Garnett, 1983). In March and May 1990, the ICBP 1990 Line and Phoenix Islands Expedition (Subchapter 1.1, Methods section) filled in minor gaps in our knowledge. Caroline’s residents added another breeding seabird, the blue-gray noddy, in summer 1990.

Methods

From 22–29 September 1988, C. B. Kepler, A. K. Kepler, D. H. Ellis, and K. Teeb’aki surveyed all of Caroline’s 39 islets except North Arundel Islet, naming most of them (Fig. 1; see Subchapter 1.1, Methods section). We established 50 linear transects, extending $13,300 \times 30$ m, laid out to ensure that at least 5% of each islet was sampled for birds and plants (see Subchapter 1.1, Methods section and Fig. 8). Sampling was increased with 19,300 m of perimeter surveys along the windward and leeward coasts of 21 islets (Subchapter 1.1, Fig. 9). On Noddy Rock, Skull, Atibu, Bo’sun Bird, Coral, Reef-flat, and Fishball (Fig. 1), we made total counts of the breeding seabirds. All surveys were conducted during daylight hours. Some incidental data have been added from the 1990 ICBP expedition.

Distribution and Habitat Preference

We described seven major plant communities on Caroline Atoll (Subchapter 1.1). With the use of aerial photos and the transect data, we mapped the communities found on each islet. Bird distribution was determined and plotted using these islet vegetation maps. If a species nested within a particular plant community, it was plotted on the distribution maps as occurring throughout that community unless determined otherwise.

Population Sizes and Breeding Phenology

We measured transect distances for each islet using a hip-chain and biodegradable cotton thread. We recorded all birds seen within the 30-m-wide strips; transect width was estimated visually. We assigned birds to one of several mutually exclusive categories: adults present, adults on territory, adults on nests (contents unknown), eggs, naked chicks, downy chicks, chicks with remiges erupting, chicks with scapular feathers, or chicks in juvenile plumage. We created a range of possible laying dates for each egg and chick using known growth parameters for each species (Kepler, 1978; Kepler & Kepler, 1978). This enabled us not only to estimate seabird populations, but also to determine and plot a rough breeding phenology for each species (Figs. 3, 5, 7, 9, 10, 12). In these figures, the height of the bar for each category (“downy,” “scapulars,” etc.) represents the number of nests found or estimated with that development stage in September 1988. The bar width represents the approximate time span over which eggs could have been laid to produce that stage, while the “no. days” is a count back from the survey dates to accommodate growth and development that had occurred. Thus, while each figure shows what breeding stages we found, we extend those nests back in time to show roughly when they would have begun. The number of clutches begun per day is determined by dividing the number of nests per stage by the time span in days over which those eggs were laid.

Sooty terns nested in dense colonies. Each colony was mapped, and its total size (m^2) was calculated. A minimum of 10 plots (3×3 m or 3×6 m), within which all eggs and chicks were counted, were randomly located along a compass line in each colony. The population size of each colony was estimated from these plot densities.

Mist Nets

We operated 4 ATX 4-shelf 36-mm mesh mist nets (2.6×12 m) for 43.5 net hours, according to the following schedule: 14.5 net hours (daylight) beneath a 10–15 m *Cocos* canopy on South, 27.5 net hours (day and night) in *Pisonia*–*Cocos* interface (12 m tall) near Tr. 10 on Long, and 1.5 net hours in *Pisonia*–*Tournefortia* within a 4–6 m canopy on Tr. 4, Long. One cuckoo was collected (USNM 607191).

Collecting Other Vertebrates

Lizards that were active and conspicuous were collected at base camps on South and Long, either by hand or with a blowgun firing steel darts. No attempt was made to search for reptiles under coral, litter, or in other concealed locations

Rats were collected with a blowgun or snap traps baited with coconut, the former proving far more effective because most traps were sprung by hermit crabs. We preserved all specimens in formalin and sent them to the US National Museum.

Seabird Species Accounts

Eleven species of seabirds occur at Caroline, most of which breed in large numbers. They include one tropicbird, three boobies, two frigatebirds, and five terns.

Red-tailed Tropicbird (*Phaethon rubricauda*) (Figs. 2,3; Pl. 1)

Red-tailed tropicbirds breed at widely scattered locations throughout the tropical Pacific and Indian Oceans. In the Line Group, they nest from Palmyra south to Starbuck (Perry, 1980), with a large population (8,500 birds) on Christmas Island (Clapp, 1967). Prior to our expedition it was unknown from Caroline, Vostok, or Flint.

Distribution and Habitat Preference: Our first indication that red-tailed tropicbirds nested on Caroline was the discovery of the skull, tail feather, and broken egg (Subchapter 1.1, Pl. 46) under a small *Tournefortia* bush on a previously unnamed islet between Pig and North Brothers Islets. We named this sparsely vegetated collection of rubble "Skull Islet" (Subchapter 1.1, Pls. 46,49). We later found 47 nests on another islet, naming it Bo'sun Bird (Fig. 1) after the species' common name.

All nests were located under relatively open *Tournefortia* scrub less than 3 m tall in open, windy locations, with the majority (91%) on small islets (0.24–0.86 ha). All nests were under shrubs with few stems within a 0.5 m² nest space, and most had peripheral cover on the sides of the shrubs, both important factors in nest-site selection (Clark *et al.*, 1983). All nests were in areas relatively free of Polynesian rats (*Rattus exulans*) and coconut crabs (*Birgus latro*): 5 nests on Long were within 50 m of the island's south point.

There are large populations of Polynesian rats and coconut crabs on Caroline's bigger, more wooded islets. This rat, though basically vegetarian, is an effective seabird predator (Kepler, 1967; Norman, 1975) that in some years has taken 65% of the red-tailed tropicbird eggs and 100% of the chicks on Kure Atoll (Fleet, 1972). Coconut crabs are also known bird predators (Clapp & Sibley, 1971a; Helfman, 1979; Reese, 1987). It may be no accident that tropicbirds on Caroline are restricted to small, relatively open islets that harbor few, if any, rats and crabs or occur only on the tip of Long Island, where predator densities are low. We saw no rats on Bo'sun Bird Islet. Although rats could swim the 165 m to the islet, the nearly continuous presence of black-tipped reef sharks (Subchapter 1.1, Pl. 10) in the channels surrounding the islet provides protection to its nesting tropicbirds.

Numbers: In September 1988, we found a total of 56 active nests on 5 islets (Fig. 2, Table 1) and estimated a minimum population of 60 pairs. The May 1990 expedition found 130 nests on Bo'sun Bird; our revised estimate for Caroline is approximately 300 birds. Bo'sun Bird Islet was surveyed by POBSP in June 1965, and no tropicbirds were located on the ground or in the air (F. Sibley, personal

communication). It is unlikely that red-tailed tropicbirds were present but overlooked at that time, suggesting that they have colonized the atoll only recently. The Caroline population is now the second largest colony known from the Line Group, and Caroline is only one of five islands in the archipelago where red-tailed tropicbirds are known to breed.

Phenology: Of the 56 nests found in 1988, 54 contained eggs or chicks (Table 2). The 33 chicks were divided into 4 age classes (Fleet, 1974; Diamond, 1975a), which, together with the 21 eggs, provided an indication of laying phenology for 140 days prior to our arrival (Fig. 3). Eggs in surviving nests had been laid at a fairly even rate from early May (possibly starting earlier) through September. The finding of only two additional pairs on territory, and only one courtship flight, indicated that laying was ending. On 24 May 1990, many nests contained eggs and downy chicks (75% nests with chicks), and pairs were still courting.

On Christmas Island, peak laying generally occurs from June to October (Schreiber & Ashmole, 1970), later than those parts of the 1988 and 1990 breeding seasons we observed on Caroline.

Masked Booby (*Sula dactylatra*) (Figs. 4,5; Pl. 2)

The masked booby is widely distributed in the Atlantic, Indian, and Pacific Oceans. Clapp (1967) estimated that 19,100 masked boobies bred in the Line and Phoenix Islands, with about 13,000 of them in the Line Islands, mostly (ca. 9,000) on Jarvis.

Distribution and Habitat Preference: Eighty-four percent of masked booby nests (159) were on the windward, rubbly shores of Long and Naked Islands, extending to the north end of the atoll. Fifteen additional nests were scattered along the lagoon edges of five South Naked Islets (Table 1). Nests consisted of bare scrapes with exposed sand, usually within a sparse ground cover of *Portulaca* and *Heliotropium* (Pl. 2). Over half the nests were amassed in one open colony on Naked that extended nearly 1,000 m, beginning approximately 150 m south of Tr. 2 and extending about 50 m north of Tr. 4 (Subchapter 1.1, Fig. 8). Here a nearly unbroken *Heliotropium* mat 30–80 m wide, with patches of *Tournefortia*, occupied the area between the leading edge of the *Tournefortia* scrub and the beach crest. Nests were 20–30 m apart in the densest section (near Tr. 3). All nests were exposed to the sun, unlike those of the brown boobies. Some adults and juveniles roosted under the scrub; guano deposits indicated regular occupancy.

A loose group of 7 breeding pairs was scattered on a broad plain of low herbs along a partially filled old interislet channel 370 m south of the north end of Long Island (Tr. C, Subchapter 1.1, Figs. 8,40). Four more pairs nested in coral rubble along the channel separating Naked and Long, one pair with a downy young only 2–3 cm above high-tide flow on an "islet" between fingers of the channel, a precarious location where nesting surely must fail in stormy periods. No birds were seen there in March and May 1990, following a severe storm in February 1990. Four pairs nested singly along a leeward 1,000-m stretch of lagoon shore on the northern end of Long (Fig. 4); hardpan was the primary substrate.

Numbers: In September 1988 we found 189 masked booby pairs (Table 3), including those on territory (with or without nest scrapes) and juveniles (with or without attending adults). We found no "clubs" of nonbreeding birds. We covered most of the habitat favored by this species except the northern 300 m of Nake Island; in 1990 a few scattered pairs nested there. Our population estimate, including pairs we might have missed, was approximately 200 breeding pairs. The only other population estimate was of "ca. 10" birds (Clapp & Sibley, 1971a); in 1965 POBSP biologists (F. Sibley, personal communication) surveyed all locations where we found breeding pairs. Thus, 200 pairs represents a major increase in the population on Caroline Atoll.

Phenology: In June 1965 only four masked booby nests containing eggs were found (Clapp & Sibley, 1971a), indicating that nesting began in May or June. We found nests in all stages in September 1988 (Table 3, Fig. 5). The large age class in April may include some juveniles that could fly (i.e., were older than 180 days). We may have undercounted naked chicks, not wishing to expose them to the sun by frightening the brooding adult. Laying began in April or earlier, peaked in June and July (Fig. 5), and continued until our survey in late September. The 34 pairs on territory, many with nest scrapes (Table 3), indicated that laying was still in progress and would continue into October.

In March 1990, 31 pairs were on territory or were attending nests, eggs, or older chicks, indicating that a new breeding season was under way as the previous season was ending. By May 1990 there were 63 nests, mostly with eggs, and there were no older chicks. Thus, the 1990 season augments the 1988 data and suggests an annual cycle with egg laying beginning slowly in February and March, peaking in June and July, and declining to a low ebb from December to February.

The large number of fledged juveniles and nests with older chicks, in both September 1988 and March 1990, indicated that the 1988 and 1989 breeding seasons were very successful. It also suggested that potential predators (rats and coconut crabs) posed little hazard to this hardy species.

Brown Booby (*Sula leucogaster*) (Fig. 2)

This widely-distributed pantropical species has an estimated population in the Line and Phoenix Islands of about 3,200 (Clapp, 1967; Perry, 1980), with over half of them (2,000) recently found on Malden Island, in the Southern Line Group.

Distribution and Habitat Preference: Breeding brown boobies on Caroline were restricted to the windward edges of *Tournefortia* scrub and forest, generally within 15–20 m of high water. In 1988 we found nests on four islets (Fig. 2, Table 1). Long, with 12 pairs, was the only islet supporting more than a single pair. They were located on the northern two-thirds of the island: four pairs formed a loose colony near the head of Tr. A (Subchapter 1.1, Fig. 8). All nests were under *Tournefortia* bushes approximately 3 m tall. In March 1990, we found 20 pairs of brown boobies, all on windward Nake as far as the islet's northern extremity. There was no evidence of nesting on Long Island. On May 22, 1990, only three nests, all with eggs, were found on Nake.

On 22 September 1988, we saw 2 birds plunge-diving with masked and red-footed boobies approximately 500 m west of South Island. On the atoll, flying brown boobies were observed soaring only along the windward beaches. Two birds roosted on the south-central beach of South, and another was found roosting on Kota.

Numbers: We counted 15 pairs during perimeter surveys in 1988, yet found none on the transects. Since we covered virtually all the windward beaches (Subchapter 1.1, Fig. 9), we are confident that fewer than 20 pairs nested on the atoll. Our population estimate for 1990 was 25 pairs.

The POBSP (Clapp & Sibley, 1971a) found three nests on Nake in June 1965, estimating a population of 15 birds. Even though our surveys triple the known population, the brown booby remains a rare seabird on Caroline.

Phenology: With the exception of one recently fledged juvenile, all nests contained eggs in September 1988 (Table 3). Clapp & Sibley (1971a) found eggs in June 1965. In March 1990, the 20 pairs were all on nests whose contents ranged from eggs to an older juvenile. However, only 2 months later, only three nests, containing eggs, could be found. These data from 3 years suggest that the species may have trouble rearing young on the atoll. More juveniles should have been encountered, especially in May 1990. Predation by Polynesian rats or coconut crabs could limit reproduction on the atoll.

Red-footed Booby (*Sula sula*) (Figs. 6,7; Subchapter 1.1, Pl. 51)

This pantropical booby numbers over 55,000 individuals in the Line Group (Clapp, 1967; Perry, 1980), making it one of the most important regions in the world for this species. Caroline holds the fifth largest known red-footed booby colony (see Nelson, 1978). The largest known colony (140,000 pairs) is found on Tower Island (Galapagos): 3 of the 5 biggest colonies occur in the Line Group.

Distribution and Habitat Preference: In 1988, the red-footed booby bred on 28 islets, ranging in size from Nautonga (0.34 ha) to Nake (107.46 ha) (Fig. 6). On the Windward Islands, red-foots occurred from Nake to Tridacna, absent only from the smallest islets (Noddy Rock, Skull Islet, Motu Atibu). The species was also widespread on the leeward islets, extending from Pandanus to Eitei. The tiny islets (Fishball, Azure, Reef-flat) were not occupied.

Red-foots are tree nesters whose distribution on Caroline closely matched that of *Tournefortia* scrub and forest (Subchapter 1.1, Pl. 51). They sometimes utilized smaller *Pisonia* or *Cordia* trees where they intermingled with *Tournefortia* and occasionally built nests in the tallest (>15 m) *Pisonia*. They nested in smaller *Tournefortia* patches within the peripheral scrublands, especially those not directly exposed to the trade winds. They clearly avoided smaller islets because of the lack of suitable *Tournefortia* in which to breed. They nested inward from the vegetated edges of the islets, generally at 3–6 m in height, and were distributed in broken rings around the smaller motus in areas of moderate winds. A higher percentage of the population occurred on perimeter surveys than on cross-island transects.

Red-foots were absent from South Island, which was primarily covered with *Cocos* (Subchapter 1.1, Figs. 50,51). Even though *Tournefortia* occurred on all its coastlines, no boobies nested in them. Ana-Ana was also unoccupied: the presence of a family of four people, a cat (removed in 1990), and a dog undoubtedly discouraged nesting attempts. Red-foots also avoided the mixed forests of south Nake, which contained much *Cocos* and *Pandanus* (Subchapter 1.1, Fig. 37). Red-footed boobies were thus found only in Caroline's indigenous woodlands, primarily in *Tournefortia* >2 m tall; they avoided anthropogenic plant communities and man.

Red-foots used a wider range of habitats for roosting. Nonbreeding birds were found throughout the taller indigenous trees, even in leeward situations where *Pisonia* and *Cordia* overhung the lagoon (as on Long Island).

Numbers: The POBSP (Clapp & Sibley, 1971a) estimated $5,000 \pm 25\%$ Red-foots on Caroline in June 1965, with about $2,000 \pm 25\%$ nesting pairs. In 1988, we sampled systematically more than 7% of the available habitat on all motus except Crescent (4.6% sampled) and North Arundel, and estimated that 2,221 pairs of red-footed boobies nested on 27 of Caroline's islets (Table 1). We found an additional 1,234 roosting, nonbreeding birds. We know (Kepler, 1969; Nelson, 1978) that fewer boobies remain in their colonies during the day than at night. Thus, an unknown fraction of the population was at sea when we conducted our counts. Impressive flights of red-footed boobies returned each evening: 3–4 birds arrived for each one that had remained behind, many undoubtedly mates of incubating birds. To approximate the number of returning nonbreeding birds, we doubled the number of roosting adults to allow for an additional 1,234 adults and juveniles. Thus, our conservative estimate was at least 7,000 individuals.

Because red-footed boobies were so dependent upon *Tournefortia*, we determined the nesting population on each islet by multiplying the number of nests found on transects by the ratio of sampled to total *Tournefortia* area. Perimeter counts (Subchapter 1.1, Fig. 9) were used if the number of red-foots observed exceeded the number calculated from the cross-island transects.

Long Island held the greatest number of nests (659), mostly in the leeward *Tournefortia* and *Tournefortia*–*Pisonia* edge. Bird densities were typically highest on the largest islets: Windward and Tridacna, the largest Windward Islets, held 163 and 111 nests, respectively; and Mannikiba, the biggest leeward islet, harbored the largest population (184) of the entire leeward side. There were exceptions, however: *Pandanus*, with four times the area of *Tournefortia* of any of the South Nake Islets, held fewer birds than three much smaller islets (Table 1).

Tournefortia scrub and forest covered approximately 125.25 ha (Subchapter 1.1, Table 9). Overall, there were 1.75 red-footed booby nests/1,000 m² of *Tournefortia* forest. Nest densities for occupied islets by island groups (Table 4) showed that red-foots favored areas less exposed to the trade winds: most nests on the windward motus were protected by well-developed *Pisonia* forests. The exposed Central Leeward Islets held the lowest nest densities (1.2 nests/1,000 m²), far less than on the South Nake Islets (5.3/1,000 m²), which are

protected by the northern edge of Long. The greatest densities (7.8 nests/1,000 m²) occurred on the South Nake Islets south of *Pandanus*.

Broadly speaking, red-foots breed in well-dispersed colonies. A record density of 600 nests/1,000 m² on Tromelin Island (Indian Ocean) is exceptional. Elsewhere, 53 pairs/1,000 m² on Tower Island (Galapagos), 40/1,000 m² on Moku Manu (Oahu, Hawaii), and 27/1,000 m² on Half Moon Cay (Honduras) are more consistent high-density colonies (Nelson, 1978). Only on tiny Motu Kota (Subchapter 1.1, Fig. 52), with 12 nests in 303 m² of *Tournefortia* (40/1,000 m²), did we find such density, and for this reason we named the islet "Kota" (Gilbertese for red-footed booby).

Phenology: In September 1988, we located 339 nests. Of the 152 whose contents could be determined, 87 were empty, 63 contained eggs, and 2 held downy chicks. We saw dozens of flying juveniles along the windward coasts. Most pairs were building or guarding their nests during a pre-laying stage that lasts from 11–35 days (Nelson, 1969). Of the pairs with nests, 57.2% had yet to lay and 41.4% had laid their eggs between mid-August and late September (Fig. 7). Applied to the total breeding population, approximately 1,270 nests were in the prelaying stage and would be expected to produce eggs throughout October. An additional 919 nests had a mean laying date in early September (Fig. 7). Red-footed boobies were synchronous with brown boobies but delayed relative to masked boobies.

In June 1965, nests containing prelaying adults, eggs, and young in all stages indicated that the birds were in the midst of a protracted breeding season extending from January to June. Our data reveal that no successful nesting occurred in May–June 1988. Data from March and May 1990 indicate that nest-building began in January (or earlier), with eggs laid from January to May. Red-footed boobies in other tropical locations have variable, opportunistic breeding seasons that depend upon food availability (Nelson, 1978); our data suggest that similar pressures could be operating at Caroline.

Color Morphs: Red-footed boobies are polymorphic (Nelson, 1978). The basic plumages are brown or white, with brown morphs having many combinations of tail, back, scapular, foot, and bill colors. A variety of brown forms and white forms occurred on Caroline, with a ratio of 9:1 (337 brown to 35 white), which contrasted sharply with Nelson's (1978) statement that "in the Line and Phoenix Islands all birds are white morphs." Most of the dark morphs were the "white-tailed" form (see Nelson, 1978, pp. 660–661). The variations and proportions of plumage types show clinal change in the Line and Phoenix Islands (F. Sibley, personal communication), and the question of plumage morphology needs much more study in the central Pacific.

Great Frigatebird (*Fregata minor*) (Subchapter 1.1, Figs. 7.8 and Pl. 42)

The great frigatebird breeds at widely scattered locations throughout tropical waters in the Atlantic, Pacific, and Indian Oceans. It is known to breed on all of the Line Islands except Starbuck (Perry, 1980).

Distribution and Habitat Preference: Great frigatebirds nested on 25 islets, including Nake, Long, and most of the larger islets (Fig. 8, Table 1), ranging in size from Azure (0.20 ha) to Nake (107.46 ha). Every occupied islet had some *Pisonia* forest, even if only a single tree (Azure). The larger islets lacking *Pisonia* forest (Arundel, 7.34 ha; Tridacna, 9.08 ha) lacked frigatebirds in 1988, although frigatebird chicks were present on Arundel in early 1989 (Anne Falconer, personal communication).

Although great frigatebirds were similar in nest requirements to red-footed boobies, there were significant differences: the frigates tended to nest higher in, and closer to, the outer edge of the canopy (although nests were found as low as 1.3 m). Nest sites were more sheltered from the wind than those of red-foots and in locations where the birds could take flight easily. Such site preferences may explain the association with *Pisonia*. *Pisonia* reaches 25 m on Caroline, taller than other tree species, providing a windbreak on most islets. The largest colonies (Nake, Long, Pig, Mannikiba) were found leeward of these stands. We found nests in *Tournefortia*, *Pisonia*, and *Cordia*. They were often in the *Tournefortia*–*Pisonia* interface, generally in the taller *Tournefortia*. One colony on south Long overhung the lagoon in a dense *Pisonia* stand. Frigates were not found in any anthropogenic forests and were absent from then-inhabited Ana-Ana.

Numbers: The previous population estimate for great frigatebirds on Caroline was 10,000 birds (Clapp & Sibley, 1971a; Perry, 1980). We calculated that 2,427 pairs bred or attended territories. An additional 617 birds roosted, thus the entire population was approximately 5,471 individuals. A large but undetermined number of birds soared over the atoll throughout the day, and an uncountable number of birds, including fledged juveniles that would ultimately return to the island to nest (Diamond, 1971), were undoubtedly at sea. Because this species is difficult to count accurately, it is unclear if the population has changed since 1965.

Phenology: In frigatebirds, the scapulars, which first appear at 81 days in *Fregata magnificens* (Diamond, 1973), erupt before the primaries. Because we lack chick stage data for *F. minor* and *F. ariel*, we have modified ages from Diamond (1973) for *F. magnificens*, using the hatching times for *F. ariel* and *F. minor* from Nelson (1976) and fledgling ages from Diamond (1975b) to construct approximate development stages for the species on Caroline. Since they fledged at an earlier age than *F. magnificens*, we have reduced the ages for chicks with erupting primaries for *F. ariel* and *F. minor*, kept the duration of the earlier stages approximately the same, and reduced the period in juvenile plumage.

We found 214 nests in 1988. Of the 144 in which we determined contents, 49 contained eggs or young chicks, 27 held chicks with developing scapular feathers, and 68 contained older chicks (Table 5). The additional 70 adults occupied nests of unknown contents; many probably held eggs or young chicks or were empty. We saw fewer than 10 displaying males, so the breeding season was winding down. This was also indicated by the high proportion (87%) of nests with chicks, many of them old. A major laying effort had

begun in March–April (Fig. 9) and continued into September. In March 1990, an abundance of flying juveniles and occasional larger chicks down to the downy stage indicated that the previous year's breeding season was ending. A small number of males were beginning another courtship cycle. By May 1990, courtship and egg-laying were still under way, and nests contained eggs or small chicks up to the "remiges" stage. Peak laying on Christmas Island (Pacific Ocean) occurs from March to May (Schreiber & Ashmole, 1970), the same laying cycle observed on Caroline in 1988 and 1990.

Lesser Frigatebird (*Fregata ariel*) (Figs. 8,10)

The lesser frigatebird is, along with *F. minor*, one of the true pantropical species. It breeds and disperses widely within the tropical Pacific (Sibley & Clapp, 1967). One of the largest populations in the world (30,000–85,000) breeds on McKean Island, in the Phoenix Group (Garnett, 1983). Lesser frigatebirds breed on four of the Line Islands, with the population on Malden (7,000) the largest in the archipelago (Perry, 1980).

Distribution and Habitat Preference: In June 1965, lesser frigatebirds were found nesting in one compact colony on the leeward north end of Long (Clapp & Sibley, 1971a). We found a single colony in leeward *Pisonia* forest on western Nake (Fig. 8), both in September 1988 and May 1990. The birds nested high (to 18 m) in the *Pisonia* and *Pisonia*–*Cordia* edge facing an open *Tournefortia* savannah. Although primarily composed of *F. ariel*, a few *F. minor* were scattered along all but the eastern edge of the colony. West of the birds, across the open forest, *F. minor* and *Sula sula* nested in a mixed colony in a denser stand of *Tournefortia*. Birds were seen soaring over Nake, Long, and the leeward islets but were not found roosting or nesting away from the colony on Nake. However, in March 1990, approximately 650 lesser frigatebirds were swarming above, and roosting on, Motu Nautonga in a tight cluster, possibly preparing for nesting.

Numbers and Phenology: Pacific Ocean Biological Survey Program biologists estimated a population of 1,000 lesser frigatebirds on Caroline in June 1965, with $400 \pm 10\%$ breeding; only eggs were found (Clapp & Sibley, 1971a). On Christmas Island, *F. ariel* laid in May and June in 1959, 1963, 1964, and 1967 (Schreiber & Ashmole, 1970). Of 46 nests found in 1988, we could inspect the contents of only 26: all contained feathered chicks (Table 5). Laying dates ranged from March through July (Fig. 10), with a peak from April to June. Caroline's lesser frigates, therefore, appeared to be synchronous with those on Christmas.

Because we did not determine the colony limits, we cannot provide a population estimate. There was a minimum of 200 birds in 1988 (46 nests, plus roosting and flying individuals) and 500 pairs in 1990.

Sooty Tern (*Sterna fuscata*) (Figs. 11,12; Subchapter 1.1, Pl. 59)

This tern is the most widespread and abundant tropical seabird in the world. Under favorable conditions it forms immense colonies numbering into the millions. It is known to breed on 7 of the Line Islands: the largest population in the

Pacific is found on Christmas Island (15,000,000 at highest count), and 3,000,000 have been recorded on Starbuck (Perry, 1980).

Distribution and Habitat Preference: To date, 19 colonies from 10 islets are known for the years 1965, 1988, 1989, and 1990 (Fig. 11). In September 1988, we found three colonies, two on the northern half of Long and one on Bo'sun Bird Islet; all fit the general habitat description in Clapp & Sibley (1971a). Colony A, nearly square, was 210 m on a side. Eggs were placed under a savannah-type *Tournefortia* scrub, from 1–4 m tall with approximately 60% canopy cover (Subchapter 1.1, Pl. 59). The substrate was coral rubble mixed with sand, covered by *Heliotropium* (5%), *Portulaca* (1%), *Laportea* (<1%), and *Lepturus* (<1%), typical of old interisland channels. Colony 1 was located in a broad sandy corridor with two large "groves" of *Tournefortia*. The northern subpopulation extended 116 m along the windward beach, but 248 m along the lagoon. The southern subpopulation began 28 m further south along the beach, fronted the seaward reef for 86 m, and was shaped like a blunt triangle, its apex pointing toward the lagoon. Most chicks were under *Tournefortia*, which consisted of shrubs 2–4 m high with 80% canopy cover. The substrate was also older beach sands mixed with coral rubble and covered with *Portulaca* (40% cover), *Lepturus* (<5%), and *Heliotropium* (<5%). The Bo'sun Bird colony, a rough oval approximately 55 m wide by 70 m long, was under 2–3 m high *Tournefortia* with 75% cover, on coral rubble/sand sparsely carpeted with *Portulaca* and *Heliotropium*.

Numbers: Populations were determined by measuring colony dimensions, then counting eggs and/or chicks in 9-m² sample plots located at random points along a compass line. Because juveniles moved as we approached, they were counted 6 m ahead of us in estimated 3 × 6 m plots. The Colony 1 subcolonies (North, South) were treated separately.

Colony size (rounded) in 1988 ranged from 127,000 ± 30,000 "nests" (Colony A) to 1,500 ± 750 new eggs on Bo'sun Bird Islet (Table 6). There were an additional 6,900 ± 1,600 nearly-fledged chicks in the Bo'sun Bird colony, resulting from eggs laid three months earlier.

The total number of eggs and chicks was 188,000 ± 21%. Actual numbers of adults are difficult to estimate but in other studies have exceeded the number of eggs and young by factors of more than two because innumerable eggs and chicks were lost, colonies often overlapped, and many nonbreeding adults joined the prebreeding swarms or associated with breeding birds. Schreiber & Ashmole (1970), relying on POBSP data from Johnston Atoll (north-central Pacific), estimated that four adults were present for each egg laid. Pacific Ocean Biological Survey Program data from Johnston (Amerson & Shelton, 1976) indicated that about 600,000 adults were present in a colony with 105,000 eggs, or approximately 5.7 adults/egg. If we assume that real numbers of terns in our colonies lay midway between 4 and 5.7 times the number of eggs and chicks, then the number of sooty terns using Caroline Atoll would have ranged between 720,000 and 1,100,000 birds (911,800 ± 21%). This is twice the estimate provided by Clapp & Sibley (1971a), even though we found fewer colonies.

In March 1990, laying was just beginning in two colonies on Long Island, (625 × 150–315 m wide and 180 × 160 m wide). Enormous numbers of birds, both on the ground in densities up to 9 or 10 pairs/m² and in the air, made it impossible to calculate a reasonable population figure. According to Anne Falconer, these two colonies were very successful. Similarly, counting was difficult in May 1990 when six large prebreeding swirls hovered like huge clouds of gnats over discrete islets and islet groups (Fig. 11). Our 1988 estimate of approximately one million birds is probably a conservative count for the atoll as a whole on an annual basis.

Phenology: The incubation period in sooty terns is about 4 weeks (Dinsmore, 1972). Young fledged 7–8 weeks after hatching, although fledgling ages, dependent upon food supply (Schreiber & Ashmole, 1970), are highly variable.

Four separate sooty tern colonies had been started over the 12-week period prior to our study in 1988 (Table 6). On Bo'sun Bird Islet a new wave of laying was just beginning in an open area immediately southwest of most of the colony, while nearly fledged chicks scurried about beneath the *Tournefortia*. Undoubtedly many young had already fledged, so many more eggs would have been laid in early July by this colony than indicated (Fig. 12). The two colonies on Long were established at different times: the short-tailed juveniles in Colony 1 preceded the large number of eggs, hatching eggs, and downy chicks of Colony A by 3–4 weeks.

The July–September laying period on Caroline in 1988 is very different from the bimodal breeding (May–June, December–January) reported from Christmas Island, Pacific Ocean (Schreiber & Ashmole, 1970), and the May laying dates noted for Caroline by the POBSP in 1965. Additional data (Anne Falconer, personal communication) indicate that sooty terns may lay any time (Fig. 11), certainly January through September (1988 to 1990). Severe storms, which destroyed large Long Island colonies in February 1990, were perhaps responsible for reinitiating breeding activities on the leeward side of the atoll within the next few months. A great deal more research will be needed on Caroline before the breeding seasons for this species are fully understood.

Brown Noddy (*Anous stolidus*) (Fig. 13)

This tern, primarily a tree nester, is widely distributed throughout the warm oceans of the world. It is abundant in the Line and Phoenix Groups, with an estimated total population exceeding 40,000 birds. Brown noddies are most abundant on Palmyra Island (10,000 birds).

Distribution and Habitat Preference: The brown noddy is second only to the white tern in the number of motus (28) upon which it is known to breed (Fig. 13). It utilized the smallest (Noddy Rock, 0.02 ha) and largest (South, 104.41 ha) motus, nesting upon coral rubble and in plant communities ranging from the simplest herb mats to *Tournefortia*, *Pisonia*, *Cordia*, *Cocos*, and the mixed anthropogenic forests of South and Nike. Most pairs were well dispersed, nesting from the outer edges of *Tournefortia* to the central, inner branches of *Pisonia*, and from the ground to the crowns of 25-m *Cocos*. When nesting sympatrically with black noddies in *Pisonia*, the brown

noddies typically occupied portions of branches closest to the trunk. Brown noddies nested almost solitarily in the *Cocos* canopy on South, were found within dense colonies of black noddies and white terns in tall *Pisonia* forests, with red-footed boobies and great frigatebirds in *Tournefortia*, and amidst sooty terns and red-tailed tropicbirds (Bo'sun Bird Islet). Apart from a few ground nesters on Raurau and Fishball, the only ground-nesting colony (80 nests) was located on a *Portulaca* mat on Noddy Rock—a site free of predators, although flooded during storms.

Brown noddies often formed loose roosting “clubs” on the atoll’s beaches. Aggregations of 15–20 birds were found on the west coast of South and on Sandy Inlet, south-central Nake.

Numbers: Clapp & Sibley (1971a) estimated a population of 1,000 birds in June 1965, with about 800 birds breeding (with eggs and young). We estimated a total population of 1,491 breeding pairs (Table 1). Because nests high in *Cocos* palms were difficult to detect, we undoubtedly overlooked many, and our estimate of approximately 3,000 birds is conservative. Although larger than the population estimated by POBSP (Clapp & Sibley, 1971a), uncertainties about the 1965 survey coverage (F. Sibley, personal communication) prevent us from knowing if Caroline’s population has changed over the past 25 years.

Phenology: On Christmas Island, the timing of egg laying varies between colonies. In general, peak laying occurs from March to May, and from November to December. On Caroline, mating and nest-building were found in March 1990, but by May only a few eggs had been laid. Eggs and young were found in June 1965 (Clapp & Sibley, 1971a) and in September 1988 (present study). We found 246 nests in September 1988 and determined the contents of 106: 103 held eggs, 3 held downy chicks. The incubation period is 35–37 days (Dorward & Ashmole, 1963), so all viable eggs had been laid within the previous 40 days (mid-August to late September). Because many nests were being built, we feel confident that laying continued into October. Clearly more research is needed to determine whether laying occurs in regular cycles.

Black Noddy (*Anous minutus*) (Fig. 14)

The black noddy is widely distributed in the tropical Atlantic and Pacific. It is abundant in the Line and Phoenix Groups, with populations of 16,000 estimated in the Phoenix Islands (Clapp, 1967) and over 46,000 in the Line Group. Centers of abundance are Palmyra (20,000) and Christmas (14,500) (Perry, 1980).

Distribution and Habitat Preference: The black noddy is a tree-nesting species that on Caroline prefers tall stands of *Pisonia*. The largest colonies (61% of the population) were found in the grand *Pisonia* forests (to 25 m) on Pig and North Pig. We found breeding birds on 18 motus, with colonies exceeding 200 pairs in the *Pisonia* on Nake, Long, Arundel, and Bird (Fig. 14). The only significant colony not primarily associated with *Pisonia* was found on Tridacna, where approximately 230 pairs nested in the tallest (ca. 8 m), most central *Tournefortia*–*Morinda* forest. Black noddies always nested in dense colonies near islet centers and were integral

components of these plant communities: their droppings, coating the ground with a film of guano, constantly enriched the islet’s meager soils.

Numbers: Clapp & Sibley (1971a) estimated that $7,000 \pm 25\%$ birds were on Caroline. During our visit the population was much larger: 5,122 pairs were estimated for Pig and North Pig alone (Table 1). Basing our numbers primarily on the densities of sampled colonies in *Pisonia*, we estimated that nearly 8,400 pairs were nesting during our 1988 visit. Our population estimate approached 17,000 birds, to which an unknown number of nonbreeding birds could be added. These values place the Caroline population far above that for Christmas, making it the largest known population in Kiribati.

Phenology: Black noddies were just beginning a new breeding season. On 27 September we observed hundreds of birds gathering *Tournefortia* leaves floating along the windward shore (Long) or flying with fresh leaves to their nests (Pig, North Pig). Of the 1,085 pairs counted on transect, 536 (49%) perched as pairs, were defending nest sites, or were building nests. An additional 273 pairs were attending nearly-completed nests but were not incubating. The remaining 276 pairs were incubating. Thus, 75% of the pairs had not laid eggs. The contents of 230 nests were unknown, although we assumed they contained eggs because of the incubating positions of the adults. Of 46 nests into which we could see, 45 held a single egg, and one contained a downy chick less than 5 days old.

The breeding seasons for black noddies on Christmas Island and Johnston Atoll peak in April and May (Schreiber & Ashmole, 1970; Amerson & Shelton, 1976), where pairs are highly synchronous, laying most of their eggs within a 2–3-month period. The Caroline colony, also synchronous, but beginning egg-production in September, would be expected to peak in October/November, six months out of phase with the colonies further north. In 1990, however, black noddies were just beginning to mate and nest in March, and by May some were still sitting tightly on nests, while others had chicks in all stages.

Blue-gray Noddy (*Procelsterna cerulea*)

Blue-gray noddies nest widely across the Pacific from the Kermadec Islands to Hawaii. They are scattered throughout the Line and Phoenix Groups. In the Line Islands, they were formerly known to breed only on Christmas and Malden (Perry, 1980). Eggs are placed in nests minimally provided with twigs and may be on coral rubble, sheltered under vegetation, or under coral slabs to depths of 1 m (Rauzon *et al.*, 1984).

The blue-gray noddy was recorded as “present” on Caroline by Perry (1980). Clapp & Sibley (1971a) noted birds over the lagoon but saw none on land. When we approached Caroline, we saw two from the ship and later observed three flying across the lagoon. We also saw three birds perched on the leeward islets, one each on the reef flats of Nautonga and Eitei. A third bird flushed repeatedly from a small clearing around a pile of bottles on Raurau, but we failed to find a nest. In March and May 1990, we observed blue-gray noddies on all of the Southern Leewards, plus Azure and Nautonga in the Central Leewards.

In summer 1990, Alexandre Falconer found one small blue-gray noddy chick, attended by its parents, on an open expanse of coral rubble on Motu Eitei, the first breeding record for Caroline. Eitei is adjacent to Raurau, which we predicted was the most likely breeding location for this species.

Blue-gray noddies evidently breed in very small numbers on Caroline. Nests are hard to find, given their cryptic placement, the small number of birds present, and the extent of open habitat (67.7 ha of herb mats and 41.4 ha of consolidated coral rubble).

White Tern (*Gygis alba*) (Fig. 15, Pl. 3; Subchapter 1.1, Pl. 55)

The white tern is a widely-distributed pantropical species occurring in moderate numbers throughout the Line and Phoenix Groups. Clapp (1967) estimated 10,000 birds in the Phoenix Group, and Perry (1980) estimated 17,050 birds for the Line Islands.

Distribution and Habitat Preference: White terns, the most widely distributed breeding bird on Caroline, nested on 32 of the 39 motus (Fig. 15). The only islets not occupied were tiny and sparsely vegetated.

White terns nested from 1 to 15 m above the ground, wherever a branch or frond provided a relatively stable platform in *Tournefortia* (Pl. 3), *Pisonia*, *Cordia*, *Pandanus*, or *Cocos* (Subchapter 1.1, Pl. 55). They did not form dense colonies but were scattered from the edge to the center of each islet, even on the windward sides, although they normally selected sites not directly exposed to the prevailing trade winds. They utilized isolated trees, scrub, or forest. An unusual departure from the white tern's usual mode of "nesting" was an egg laid in an old black noddy nest, 6 m up in an 8-m-tall *Tournefortia* on Tridacna Islet.

White tern densities varied from islet to islet (Table 7). At one extreme, we found only two nests on Raurau (0.07/1,000 m²). Densities on other islets ranged from 0.75/1,000 m² (Shark) to 6.67/1,000 m² (Nautonga) with a mean density of 1.38 pairs/1,000 m² of woodland. Overall, the Windward Islets supported the highest densities. Although white terns also nested in anthropogenic forests, their densities were low: we believe that the low densities on South Island and the Southern Leewards (Table 7) are attributable to man. Of South's 104.47 ha of vegetated land, only 4.2 ha (4.4%) was native woodland (Subchapter 1.1, Fig. 50); fully 84% was either *Cocos* (18.3 ha) or *Cocos-Ipomoea* (62.5 ha) forest. Although most of the Southern Leewards are covered in unmodified natural forest, central Ana-Ana has been partly cleared (0.21 ha) to accommodate thatched huts and a garden. The activities of a family of four, with a dog and cat (until October 1990), have apparently depressed the white tern population on Ana-Ana and, perhaps, even on nearby islets. We found no white terns on Ana-Ana during our visit, although the Falconers, who vacated the atoll in summer 1991, assured us that they occasionally nested.

Numbers: We used the total woodland area of each islet to calculate islet populations (Table 1) from our transect data. More birds were found on the largest islets except South Island. We estimated 1,094 pairs for Nake, 751 pairs for Long, and nearly 400 pairs for Tridacna; these 3 islets accounted for over

half the population (and over half the native woodland). We estimated that 3,957 pairs bred on Caroline. This doubles the numbers of Clapp & Sibley (1971a) and cited by Perry (1980) and exceeds by 3,000 the largest population formerly known for the Line Islands.

Phenology: Of 569 pairs of white terns recorded on transect, 437 were roosting without obvious signs of eggs or chicks, 107 were incubating, and 25 had chicks (often adults were not present). Of the 25 chicks recorded, 17 were downy, 7 retained extensive traces of down with remiges, and 1 was almost ready to fly. Incubation takes about 36 days (Ashmole, 1963); young may require from 40 to 96 days to fledged (Gibson-Hill, 1950; Ashmole, 1968). Nearly all chicks were far from fledging and were less than 4 weeks old.

On Christmas Island, Schreiber & Ashmole (1970) found that peak laying occurred in April–August each year, with some laying in each month. On Caroline, Clapp & Sibley (1971a) noted that about half of the birds had eggs, half had young in June 1965. In March 1990, we found only a few eggs and downy chicks, but in May a larger number of pairs were breeding, with eggs and chicks in all stages. Although we found that white terns on Caroline do lay during the peak period on Christmas, it was clear that in 1988 most eggs were laid after mid-August.

Other Birds on Caroline Atoll

Seven species other than seabirds have now been recorded on Caroline. Six of them are migrants (five shorebirds and a long-tailed cuckoo). The reef heron is apparently resident, although no nest has yet been found.

Reef Heron (*Egretta sacra*)

We found 15 reef herons scattered on 8 islands: Nake (1), Long (2), Pig (1), Brothers (3), South (2), Mannikiba (2), Matawa (1), and Emerald (2), as well as on the open reef flats (1). Although birds were found on both the seaward and lagoonward sides of the islets, most were along the lagoon edge, as also found by POBSP in 1965 (Clapp & Sibley, 1971a). We estimated that approximately 30 birds were using the atoll. We found no signs of breeding. Of the 15 individuals we observed, 5 were dark, 8 were white, and 2 were of the pied morph.

Lesser Golden-plover (*Pluvialis dominica*)

This plover used the beaches and herb mats, generally to seaward. In September 1988, we found them on Nake (1), Long (4), Tridacna (4), and Mannikiba (1), estimating a total population of 20–30 birds, the same number found by POBSP (Clapp & Sibley, 1971a). In March 1990, we observed eight, and in May, three, all in winter plumage.

Wandering/Siberian Tattler (*Heteroscelus incanum* or *H. brevipes*)

In September 1988, we located 18 tattlers on 6 different islets: Nake (3), Long (3), Crescent (1), Arundel (2), South (7), and Emerald (2). All birds were either alone or in pairs and generally remained in the intertidal zone, although they often

foraged on herb mats close to the beach scrub. The total population was approximately 40 birds. Those few birds heard were all *H. incanum*. We saw six tattlers in March 1990 and several in May of the same year.

Ruddy Turnstone (*Arenaria interpres*)

One turnstone was found on the windward beach of Motu Mannikiba in September 1988, and five on atoll beaches in March 1990. The Caroline population probably does not exceed 15 birds.

Bristle-thighed Curlew (*Numenius tahitiensis*) (Subchapter 1.1, Pl. 23)

The bristle-thighed curlew, common in the Line and Phoenix Groups, is a widespread migrant to the low atolls of the central and South Pacific during the boreal winter (Pratt *et al.*, 1987). One of the world's least-studied shorebirds, the species is considered rare throughout its range (Johnsgard, 1981; Marks *et al.*, 1990) and is a candidate for the US Fish & Wildlife Service Endangered Species List (Gill, 1990). Clapp & Sibley (1971a) estimated 20 birds for Caroline in June 1965.

We counted 83 birds on 12 of Caroline's islets in 1988, including the 3 large islands (Nake, Long, South) and motus in the Windwards, Central Leewards, and Southern Leewards. In March 1990, we saw 20 curlews on 10 islets during incidental observations throughout the atoll, bringing the total number of islets on which they have been recorded to 16. On our return trip (May 1990) we only saw three curlews (only eight islets visited). Undoubtedly, curlews occur on all islets, utilizing essentially all plant communities. Although they are most conspicuous on the beaches and reef flats, higher numbers may actually forage in the forests during the day. The Falconers (personal communication) note that small numbers of curlews remain all year. They are least common between April and August and most abundant after September/October. This correlates with preliminary information from Rangiroa Atoll, Tuamotu Archipelago (Gill, 1990; Gill & Redmond, in prep.).

Perimeter Habitats: On a complete perimeter count of South Island in 1988, we found 29 curlews. Twenty-one were foraging and loitering on the windward east coast, principally above the beach crest on coral rubble interspersed with herb mat. Similarly, 14 of 20 curlews found on Long and the Windward Islets foraged along the windward beach crest, with only 6 birds found on the lagoonward shores. Curlews were equally common on windward and leeward shores in the leeward islets, occupying habitats composed of coral rubble and sand. While the numbers indicate that curlews showed a preference for windward shores, they may be biased because most birds were there in late evening (19 birds on South). Perhaps they use the relatively open areas for roosting and foraging at dusk. Certainly the largest concentrations (13, 14) were found late in the day. We found our largest flock (14, Sandy Inlet, Nake) at 1600 h, foraging on compacted, silty sand at the lagoonward end of the inlet, while single curlews dotted the interislet channels and shallow tidal reef flats.

Vegetated Habitats: We found bristle-thighed curlews on natural herb mats, in *Tournefortia* scrub, *Pisonia* forest, and in

Cocos habitats, both in the healthy peripheral plantations and within the dying *Cocos-Ipomoea* woodlands (Subchapter 1.1, Fig. 36, Pl. 34). One was captured in a mist net under a dense *Cocos* canopy. Disintegrating plantations in the center of South (54 ha) held a large population: calculated numbers produced an estimate of 154 curlews. They foraged over the *Ipomoea*-strewn ground, frequently using broken-topped coconut trunks as lookouts. We also found 5 curlews on transects in *Pisonia* forests up to 20 m tall on Nake (calculated population, 41). They were foraging on the relatively open, although dimly lit, forest floor.

Numbers: From the 1988 data we estimated a population of ± 300 curlews: 41 birds in *Pisonia*, 154 in *Cocos-Ipomoea*, 43 on the beaches of South Island (29) and the Sandy Inlet of Nake (14), and another 62 scattered over the remainder of the atoll. Because 154 of them were calculated from the sighting of a flock of 7 curlews on one transect on South, there may be a bias in our population estimate. Incidental observations made off-transect did show, however, that curlews were common in the *Cocos-Ipomoea* woodlands, and we believe that the numbers on the 104 ha that compose South Island approximated our estimated density (about 1.5 birds/ha).

Bill Length: Bristle-thighed curlews show great variation in bill length immediately after the breeding season. Because birds of the year migrate south before their bills reach adult length (R. Gill, personal communication), the ratio of "long" to "short" bills provides a rough estimate of juvenile survival. Of 31 curlews seen in September, 20 were clearly adult length, 7 were conspicuously shorter, and 4 were "intermediate" (probably young birds). All March and May birds had long, adult-sized bills.

Some subadults also remain on their Pacific wintering grounds for up to 3 years, during which time they pass through a flightless phase (Gill, 1990; Marks *et al.*, 1990). No flightless birds were seen.

Foraging: We saw one curlew chase and capture a small Polynesian rat at dusk on the south shore of South Island. The bird bashed the rat on the coral rubble, then ran rapidly about with the rat dangling from its bill. After about 5 minutes, the bird swallowed the rat with vigorous gulps.

Polynesian rats, abundant on Caroline (especially in *Pisonia*- and *Cocos*-dominated habitats), remain within the forest during the day, but many move to the beach crest and tide line at dusk. They provide abundant potential prey for curlews, which can easily capture them on the open rubble. The synchronous appearance of rats and curlews at the beach-woodland interface at dusk may be part of the foraging strategy of this large shorebird. The presence of curlews beneath the forest canopy may also be partly associated with this source of food.

Sanderling (*Crocethia alba*)

One sanderling in winter plumage was seen at water's edge on the windward beach of Long Island on 27 September 1988. Although Sanderlings are well-known fall migrants in the Line and Phoenix Islands (Clapp & Sibley, 1967, 1968), this is the first record for Caroline Atoll.

Long-tailed Cuckoo (*Eudynamis taitensis*) (Fig. 16)

The long-tailed cuckoo breeds in New Zealand and winters in the southwest Pacific. The center of its winter range lies in central Polynesia, but birds have been recorded as far as Palau in the northwest and Pitcairn Island in the southeast. Although occurring throughout French Polynesia and the Cook Islands, it had not been recorded from the Line Islands prior to our expedition (Bogert, 1937; Clapp & Sibley, 1971a,b; Pratt *et al.*, 1987; Ellis *et al.*, 1990).

We found long-tailed cuckoos on 4 of Caroline's 39 motus (Fig. 16). We heard its distinctive monosyllabic and disyllabic call notes on South, Long, and Pisonia, identified one on Nake, and on 28 September collected a male in a mist net on Tr. 4, Long Island (USNM 607191). Soon after our return home we sent a description and photograph of this species to the Falconers; they, and AKK, have since seen them several times on Motu Ana-Ana in March, April, and May 1989–90.

All the cuckoo sightings were at canopy or subcanopy level, and three of the four birds were found in *Pisonia*. The South Island cuckoo was located in a *Cocos* canopy over 20 m high. The netted male flitted secretively within an undisturbed, tangled low-canopy (4–6 m) *Pisonia*–*Tournefortia* interface. We suspect that this elusive migrant occurs throughout the mid-to-upper levels of Caroline's forest canopy.

These records establish the long-tailed cuckoo as a winter visitor to Caroline Atoll. Our observations on four islets, including the southernmost, northernmost, windwards, and leewards, suggest that many individuals were present. A March 1990 first sighting on Vostok (J. Phillips, personal communication) further suggests that the species disperses regularly to the Southern Line Group.

Other Vertebrates

Lizards

Although "small lizards" were observed on Caroline in 1825 (Paulding, 1831), it wasn't until 1965 that the first collections were made (Clapp & Sibley, 1971a). We collected four additional lizard species, which increased the known terrestrial herpetofauna from three to six (Table 8). Although all are indigenous, the azure-tailed skink (*Emoia cyanura*) is suspected of being partly dispersed by man (Brown, 1956). All but two of the small lizard species known from the Line Islands (Crombie, 1990) have now been found on Caroline.

Turtles

We found three Pacific green sea turtles (*Chelonia mydas*), a threatened species (McKeown, 1978), at Caroline in 1988. Two were swimming over the lagoon reef flats, one west of Arundel, the second east of Ana-Ana. The third was in the open sea about 100 m west of South Island near the "boat entrance." Ron Falconer has seen up to seven turtles in the lagoon in a single day. In April and May 1990, AKK saw workers from Tahiti capture and kill a minimum of four green turtles in the lagoon; two more entered the lagoon during the following 4 months (R. Falconer, personal communication).

In March 1990, AKK and G. Wragg found three old nests, presumably of this species, on the northwest coast of Nake within 100 m of the northern tip of the islet. These are the first known turtle breeding records for the atoll. Young (ca. 1922) notes that the copra plantation laborers ate green turtles from September to December each year. The February 1990 storm added large amounts of sand to Caroline's shorelines, providing potential new habitat for turtle nesting.

Terrestrial Mammals

None of the terriers (see Subchapter 1.1) that were introduced to control rats on South Island in the early part of this century (Young, ca. 1922) have survived (F. Sibley, personal communication; R. Falconer, personal communication). In May 1990 the Falconers kept a dog and a cat on Motu Ana-Ana. Despite the fact that both animals generally remained close to the settlement, the dog regularly visited the other Southern Leeward Islets and accompanied the family on excursions in their sailing canoe throughout the atoll. As a result of our recommendations, the cat was removed from Caroline in October 1990. The Falconers, with their dog, vacated the atoll in mid-1991.

Bennett (1840) noted "rats of a red-brown color," the first reference to rodents on Caroline. Dixon (1884) found that rats were "not numerous" and that they nested "just at the base of the fronds" of the coconuts. Two specimens collected by the POBSP proved to be *Rattus exulans* (Clapp & Sibley, 1971a). They reported that rats were uncommon and restricted to South Island.

The 19th and 20th century settlers found rats (presumably *R. exulans*) to be extremely abundant and very destructive to the coconut plantations. Maude (ca. 1938) states that rats destroyed the nuts, and that they contributed greatly to the eventual abandonment of copra enterprises on Caroline and Flint. They voraciously devoured both growing and fallen nuts, as well as dried copra. Being arboreal, they also lapped the juices of the flower stalks, preventing nut development (Young, ca. 1922). In a single year (1920) over 4,600 were trapped on South Island (Maude, ca. 1938). Thousands more were killed by terriers introduced to Caroline in a vain attempt to control them.

We found rats on almost every islet; they were especially abundant on South, Long, Nake, and in the vicinity of coconut palms on smaller islets. We recorded rats during daylight hours on most transects, especially within the *Pisonia* forests. At our campsites on Long and South we noticed groups of 10–20 each night, so tame as to approach within 1 m while we were eating. The rats evidently undergo wide population fluctuations, as they were less abundant in March and May 1990 than in September 1988.

We suspect that rats periodically reach most motus, and that the islets apparently lacking rats (such as Noddy Rock) are too small and/or depauperate to support a resident population. Because *R. exulans* is a known seabird predator (Kepler, 1967; Fleet, 1972; Norman, 1975), the restriction of some species (i.e., red-tailed tropicbird) to small islets may be due to rat populations on larger islets.

We found rats throughout the Southern Leeward Islets and learned from the Falconers that they are an abundant nuisance on Ana-Ana. They trapped over 1,300 animals in 2 years and, like the pioneers before them, rely upon a dog to help keep them at bay.

Marine Mammals

On March 14, 1990, members of the Line and Phoenix Islands Expedition observed a minimum of 10 Pacific bottlenose dolphins (*Tursiops gilli*) in the open sea about 500 m off the southeast corner of South Island.

Coconut Crabs

The coconut crab (*Birgus latro*, Coenobitidae), the largest terrestrial invertebrate on earth, ranges throughout the tropical Indo-Pacific (Subchapter 1.1, Pl. 56). It is highly esteemed as a source of food throughout its range, and for this reason is rare or absent on or near most inhabited islands. Because it is heavily exploited by man, it is under consideration for endangered species status (Reese, personal communication). Since March 1990, dozens of Caroline's coconut crabs have been killed for food and for preservation in formalin as curios for the Tahiti tourist market. Because of the increasing numbers of visitors to Caroline over the past 2 years, it is important that Caroline's coconut crabs receive protection.

History: Young (ca. 1922) was the first to mention coconut crabs on Caroline. In 1910 he wrote that "hundreds of great Coconut Crabs were seen: 40 large ones were caught by the crew of the schooner in an hour" on South Island.

It is hardly credible that these enormous crabs, the dominant terrestrial animal of the atoll environment, could have been overlooked by all visitors prior to the 20th century. Perhaps their populations had been reduced or extirpated by earlier inhabitants. It is of interest in this regard that members of the 1934 Mangarevan Expedition saw no coconut crabs on nearby Flint Island (Fosberg, personal communication), nor were they mentioned in a historical summary paper on Flint by Maude (ca. 1942b). Today Flint has perhaps the greatest density of coconut crabs in the world (Kepler, 1990b).

Young (ca. 1922) noted that coconut crabs were considered a great nuisance by plantation laborers, who killed them mercilessly. Evidently the crabs dug up newly planted nuts and snipped off emerging shoots. On the smaller islets, visited less frequently than South, Nake, and Long, these depredations were difficult to control. Thus the small motu plantations were abandoned within a few years of initial planting, resulting in a remarkably rapid recovery of the original vegetation (see Subchapter 1.1, Ecological Succession section).

Distribution and Habitat Preference: In 1988 and 1990, coconut crabs were abundant in the *Cocos* plantations of South and Nake, and present, in varying densities, on 12 other motus (Fig. 18). Although generally associated with *Cocos*, we found them in woodlands of *Pisonia*, *Cordia*, and *Tournefortia*, as well as on rubble beaches (especially after dusk). Although capable of surviving without coconut palms, these crabs appear to seek them out. In the open understory of the tall plantations,

or in groves of only one or two palms, telltale piles of shredded coconut husk fibers (Subchapter 1.1, Pl. 57) disclosed the crab's presence.

Because the prevalent coarse rubble substrates on Caroline are hard to burrow into, coconut crabs occupied a variety of shelters: mounds of fallen coconuts and rotting palm fronds (to 1.5 m high), piles of rubble pushed against tree roots, sand burrows, tunnels within the *feo* (Subchapter 1.1, Pl. 22), or large cavities in the boles of mature *Pisonia* trees. Coconut crabs also use a variety of shelters on the Tokelau Islands (Yaldwyn & Wodzicki, 1979) and Flint (AKK, personal observation).

Numbers: Though conspicuous and slow-moving, coconut crabs are very difficult to count. Environmental variables such as rainfall, tide, lunar cycle, and population size and age classes all affect their activity (Reese, 1965; Helfman, 1977a,b). Although unable to conduct mark-recapture studies, we did make incidental observations on the numbers of individuals seen during transect and perimeter surveys. Coconut crabs are generally nocturnal, but we often found them during daylight, at times exposed on coral gravel beaches close to the waterline. Reese (personal communication) suggests that the abundance of rats occupying the same habitat may "force" the crabs to be more diurnal, as has been reported from the Indian Ocean. Our estimate of the population on Caroline is approximately 2,200 individuals, based on the number of daytime observations, the area covered, and the fact that only one out of every three or four individuals may be present on any given night (Helfman, 1977b; Reese, 1987).

Foraging: Since the first detailed description of coconut crabs in 1705, their shy, curious habits have been the subject of folklore, speculation, and misinformation (see Reyne, 1939). No scientist has yet published a documented account of a coconut crab actually opening a coconut (Helfman, 1979), which is widely held to be their consummate foraging behavior. Helfman is convinced that they do so, as he has found piles of coconut fiber and observed crabs walking with husked, opened nuts in places where he was the only other possible coconut husker. We repeat Helfman's (1979) assertion that coconut crabs *do* husk fallen coconuts. The piles of finely separated fibers (Subchapter 1.1, Pl. 57) we encountered are totally different from those produced by stick or machete husking, the two methods commonly employed by Pacific peoples. The crab tears virtually every fiber off individually, a process so painstakingly slow it probably takes days. We did not observe this on Caroline, but in March 1990, AKK, on uninhabited Flint Island, observed a large male coconut crab that had just husked a coconut and was enlarging a small crack in the center of the smooth nut in a manner similar to that described by Gardiner (1907) in Reyne (1939, p. 297).

On Caroline we observed the aftermath of coconut crab/sooty tern predation or scavenging. On Brothers Islet, several entrances and pathways leading to coconut crab holes were strewn with the feathered skeleta of adult sooty terns (and possibly brown noddies), along with numerous, freshly snipped branches of *Pisonia* up to 0.7 m long (Subchapter 1.1, Description and Ecology of the Motus section). This was also

recorded on Tridacna Islet by Clapp & Sibley (1971a) for sooty tern eggs and chicks and by Reese (1987) and Helfman (1979) on Enewetak, Micronesia.

Size: Living in a rich environment free of predators, coconut crabs attain huge sizes on Caroline. The bodies of the largest males were as wide as a full-sized, unhusked coconut (Subchapter 1.1, Pl. 56), giving them weights of at least 4 kg (Helfman, personal observation). Thorax widths for 10 crabs (2 females with eggs, 8 males) averaged 129 mm. The thorax of the largest male measured 200 mm across, making it, along with many measured on Flint in 1990, one of the largest recorded coconut crabs in the world (the previous record was 178 mm, Helfman, 1977a), with an age estimated to exceed 40 years (E. Reese, personal communication).

Conservation: Attributes of International Significance

When Bennett (1840) stated that “no reefs we had seen could compete with those of Caroline for novelty and beauty,” he was seeing an essentially pristine ecosystem through the eyes of a well-traveled naturalist. Caroline is stunning, but its value in today’s shrinking world goes well beyond its physical beauty. Caroline’s exceptional attributes need to be elucidated, for the atoll has remained essentially unknown, even to some who have evaluated its worth (King, 1973; Garnett, 1983, 1984). Man’s presence anywhere, especially on pristine or near-pristine islands, generally brings rapid, often irreversible, changes. There are few, if any, islands remaining in the Pacific that can claim the impressive array of natural features exhibited by Caroline (Nicholson & Douglas, 1969). We believe that it is imperative that this atoll, which has managed to escape large-scale human disturbance, should remain undeveloped.

Caroline was inhabited from 1988 to 1991 by a single family who lived a spartan, ecologically sound lifestyle. There are no roads, vehicles, stores, jetties, or services (water, sewage, or food), and no communication. There is no passage into the lagoon or safe sea anchorage.

One of the most important of Caroline’s attributes is its relative lack of disturbance. Aside from obvious human impacts on South, Nake, and Ana-Ana, the majority of its motus are dominated by indigenous vegetation and its reefs are basically pristine. There is no obvious pollution to alter the chemistry of the lagoon, beyond the flotsam and jetsam that spatter the windward beaches. It is thus an exceptionally clear and clean ecological laboratory that presents a picture of lagoon ecosystems “before” extensive disturbance by man, and one that provides the marine biologist with an unparalleled opportunity to study undisturbed natural communities. The atoll is rich in marine vertebrates and invertebrates; the maze of reefs and coral heads in the lower half of the lagoon has the highest recorded density of living *Tridacna* (20/25 m²) ever recorded (Sirenko & Koltun, Subchapter 1.4, this volume), one of the few undisturbed world populations of this species (Subchapter 1.1, Pl. 26).

Caroline’s many islets of different sizes provide excellent examples of soil and vegetation development, accompanied by variations in the diversity of bird life (Fig. 17). Many of its

disturbed islets have recovered so remarkably they are almost indistinguishable from those which have remained pristine. The changing shapes of the islets, bearing emerging and mature plant communities, graphically portray a natural terrestrial atoll ecosystem. Caroline’s concentric pattern of plant community development and the relationships of these communities to islet size, shape, and location on the atoll rim will continue to provide insight into evolutionary processes on atolls if they are left undisturbed.

Caroline’s insular flora, typical of central equatorial islands in their natural state and covering 70% of the atoll’s land area, is of both national and international importance. The 27 extant plant species are 85% indigenous (possibly up to 93%), an extremely high figure for anywhere in the world. Six of the seven plant communities are natural. Lushly wooded, Caroline possesses some of the largest and grandest *Pisonia* (*Pisonia grandis*) forests known (Subchapter 1.1, Pl. 43), occurring on 29 islets. Although not as majestic as the prime forests on Washington and Fanning (Northern Line Group), which enjoy a heavier rainfall, those on Caroline are some of the finest representatives of this forest community in the entire Pacific. The 62 ha of *Pisonia* forest may well cover a larger area than on any other Pacific atoll.

Caroline possesses significant stands of the hardwood *kou* (*Cordia subcordata*), a tree that is now rare in the Pacific. Caroline’s groves (Subchapter 1.1, Pl. 27), though small and often occurring in mixed native woodlands, total 26 ha, possibly the greatest area on any Pacific atoll. Its extensive coverage of tree heliotrope (*Tournefortia argentea*) is also notable: scrub and forests of this species form 40% of the atoll woodlands (Subchapter 1.1, Pl. 47). Caroline’s groves are some of the most unmodified in the Pacific; elsewhere *Tournefortia* is typically restricted to coastal fringes surrounding anthropogenic plantations (R. Fosberg, personal communication).

Caroline offers many opportunities for ecological research under reasonably pristine conditions. Valuable clues as to the nature of underground water supplies may lead to a better understanding of the regulation of water supplies on inhabited islands. Marine biological and biomedical research could unearth clues as to the causes and treatment of ciguatera toxicity of fishes and crabs. Such topics are increasingly important as more islands are subjected to disturbance and pollution. For example, the abundant red snapper (*Lutjanus vaigiensis*) and red spotted crab (*Carpilius maculatus*), both of which are notorious for their potent poisons, are safe to eat on Caroline.

Associated with Caroline’s plant communities are 11 species of breeding seabirds numbering well in excess of 1,000,000 individuals. The populations of most of these species are of national importance (Table 9). Caroline has the fifth largest red-footed booby colony (Subchapter 1.1, Pl. 51) in the world. Its black noddy and white tern (Pl. 3) populations are the largest in Kiribati. Under the 1975 Republic of Kiribati Wildlife Conservation Ordinance (amended in 1979), all known seabirds, migrant shorebirds, and endemic land birds are “fully protected throughout the Gilbert Islands” (Garnett, 1983, p. 128). However, their protected status is in doubt on Caroline, due to attempts to lease the island for development.

Caroline deserves protection similar to five closed areas on Christmas Island and seven island sanctuaries in the Line and Phoenix Groups (Garnett, 1983).

Caroline is an important wintering ground for the bristle-thighed curlew, a rare shorebird and candidate for the US Fish & Wildlife Service Endangered Species list. Some subadults remain all year on the atoll. Adult curlews pass through a flightless phase on Pacific islands, and Caroline provides a predator-free environment for this vulnerable phase of the curlew's life history.

Caroline is exceptional in harboring a robust population of coconut crabs (Subchapter 1.1, Pls. 22, 56). These large invertebrates are abundant in the *Cocos* plantations of South and Nake and are found in good numbers in the indigenous *Pisonia* forests on most of Caroline's larger motus.

Although green turtles are not abundant on the atoll, worldwide populations of these marine reptiles have suffered so greatly from overexploitation that remote, predator-free islands such as Caroline provide important, though small, sanctuaries. Since 1978 the Pacific green sea turtle has been reclassified by the United States Department of the Interior as threatened and the Pacific hawksbill sea turtle as endangered.

From an archaeological point of view, Caroline houses one intact Tuamotuan *marae* (ancient religious site) and another smaller site, partly destroyed by storms. The main site (Subchapter 1.1, Fig. 3, Pl. 36), basically undisturbed since the 1870's, is a relic of prehistoric occupation worthy of protection, being the only one of its kind in the Line and Phoenix Islands.

Currently Caroline Atoll is owned by the government of the Republic of Kiribati and does not enjoy any legal protection (Garnett, 1983; Government of Kiribati, personal communication). Over the last 50 years it has been leased to private individuals who have scarcely altered the atoll. The benign management of the past is no guarantee for the future, and from October 1989 to the present, pressures to develop the

atoll have mounted rapidly. Proposed schemes included an airstrip, a blasted channel through the reef, a hotel, a casino, logging, and commercial harvest of fish and lobsters. In March 1990, commercial harvesting of fish, the taking of coconut crabs, and illegal killing of green turtles began, emphasizing that no island, however remote, is guaranteed protection through isolation. In addition, during the past 2 years Caroline has become more visited than ever before, mostly without the knowledge or consent of the Kiribati government.

There are many reasons why Caroline is inappropriate for resident tourists or development (remoteness, distance from medical aid, no regular water supply, no passage into the lagoon, etc.; see Kepler, 1990a). Caroline could support a limited number of ship-based ecotourists each year.

Recommendations for an international preserve began in January 1989. During the 1990 ICBP expedition to the Line Islands, the team leaders discussed conservation matters with Kiribati government officials and key scientists in French Polynesia. Fortunately, documentation was obtained of illegal land clearing and wildlife disturbance during two visits to Caroline (Kepler, 1990a,b,c). The Kiribati government is considering altering their plans for the development of Caroline in favor of wildlife preservation. During summer 1990, French customs officials in Tahiti temporarily banned the exploitation of Caroline by French Polynesian nationals.

As of December 1990, The Nature Conservancy of Hawaii has restated its interest in establishing a triple-island preserve on Caroline, Vostok, and Flint and has begun discussions with the Kiribati government on Tarawa. The fate of these special islands may rest upon the results of these negotiations.

We have a number of people to thank for their assistance in this project; however, our acknowledgments for Parts 1 and 2 of the manuscript, *Ecological Studies of Caroline Atoll, Republic of Kiribati, South-central Pacific Ocean* are listed at the conclusion of Part 1, and are not repeated here. Again, it is our sincere pleasure to thank these individuals.

TABLE 1

Estimated number of breeding seabird pairs on Caroline Atoll, September 1988.

<u>Location</u>	<u>Red-tailed Tropicbird</u>	<u>Masked Booby</u>	<u>Brown Booby</u>	<u>Red-footed Booby</u>	<u>Great Frigatebird</u>	<u>Lesser Frigatebird</u>	<u>Sooty Tern</u>	<u>Brown Noddy</u>	<u>Black Noddy</u>	<u>Blue-gray Noddy</u>	<u>White Tern</u>
Nake	-	105	1	496	522	56	-	390	814	-	1,094
Long	5	69	12	659	808	-	179,800	207	986	-	751
Windward Islets											
Bo'sun Bird	47	-	-	-	-	-	8,400	10	-	-	6
Windward	-	-	-	163	207	-	-	20	28	-	134
Crescent	-	-	-	28	5	-	-	36	60	-	8
Atibu	-	-	-	-	-	-	-	-	-	-	-
North Pig	-	-	-	31	17	-	-	76	3,194	-	110
Pig	-	-	-	14	118	-	-	82	1,928	-	164
Skull	-	-	-	-	-	-	-	-	-	-	-
North Brothers	-	-	-	25	9	-	-	23	40	-	69
Brothers	-	-	25	-	-	-	-	8	15	-	50
Noddy Rock	-	-	-	-	-	-	-	80	-	-	-
North Arundel	-	-	-	*	*	-	-	-	-	-	*
Arundel	-	-	-	37	*	-	-	11	249	-	227
Tridacna	-	-	1	111	-	-	-	11	230	-	396
South	-	-	-	-	-	-	-	163	-	-	381
South Nake Islets											
Pandanus	-	2	-	32	26	-	-	26	-	-	52
Danger	-	-	-	139	-	-	-	33	33	-	37
Booby	-	7	-	52	-	-	-	2	1	-	6
Coral	-	1	-	28	2	-	-	6	-	-	15
Lone Palm	-	2	-	48	-	-	-	-	-	-	9
Kota	-	-	1	12	1	-	-	-	-	-	3
Mouakena	-	3	-	8	-	-	-	-	-	-	-
Central Leeward Islets											
Mannikiba	-	-	-	184	287	-	-	161	176	-	195
Blackfin	-	-	-	*	4	-	-	37	-	-	11
Matawa	-	-	-	5	1	-	-	3	-	-	13
Emerald	1	-	-	3	230	-	-	7	150	-	83
Shark	-	-	-	*	118	-	-	37	125	-	44
Scarlet Crab	-	-	-	-	-	-	-	1	-	-	2
Nautonga	-	-	-	11	2	-	-	7	32	-	10
Azure	-	-	-	7	2	-	-	-	-	-	2
Reef-flat	-	-	-	-	-	-	-	-	-	-	-
Bird	-	-	-	29	6	-	-	42	329	-	48
Fishball	3	-	-	-	-	-	*	5	-	-	-
Southern Leeward Islets											
Raurau	-	-	-	10	31	-	-	1	-	-	2
Eitei	-	-	-	17	14	-	-	6	-	*	18
Pisonia	-	-	-	26	14	-	-	-	-	-	10
Kimoa	-	-	-	21	3	-	-	-	2	-	7
Ana-Ana	-	-	-	-	-	-	-	-	-	-	-
Total Estimated Pairs	56	189	15	2,221	2,427	56	188,200	1,491	8,392	-	3,957

* Breeding confirmed in 1989 or 1990.

TABLE 2

Stages in the breeding cycle of the red-tailed tropicbird, Caroline Atoll, 27–29 September 1988 (ages after Stonehouse, 1962).

Nest Stage	Approximate Age in Days From Laying	No. Nests
Juv.	90-133	18
Remiges	69-89	4
Scapulars	58-68	5
Downy	44-57	6
Egg	0-43	21
Pairs on Territory	-	2

TABLE 3

Stages in the breeding cycle of the boobies of Caroline Atoll, 21–29 September 1988.

Species	Nest stage ¹ /Approximate age in days from laying							Pairs on Territory
	Flying Juv.	Juv.	Scapulars	Remiges	Downy	Naked	Eggs	
Masked	>164	145-164	115-144	89-114	55-88	45-54	0-44	
Brown	>164	144-164	114-144	88-114	54-88	44-54	0-44	
Red-footed	-	>150	111-150	75-110	54-74	45-53	0-45	
No. nests in each stage								
Masked	-	40	12	22	38	4	33	34
Brown	1	-	-	-	-	-	3	8
Red-footed	many	-	-	-	29	-	919	1,270

¹ For descriptions of nest stage, see C. B. Kepler (1978).

TABLE 4

Density of red-footed booby nests in occupied *Tournefortia* habitats on islet groups, Caroline Atoll, September 1988.

Islet Group	Number Occupied Islets	Estimated Number Nests	Area of <i>Tournefortia</i> (m ²)	Nests/1,000 m ² of Available Habitat
Nake	1	496	300,650	1.6
Long	1	659	322,000	2.0
Windward Islets	8	434	251,900	1.7
South Nake Islets	7	319	59,800	5.3
Central Leewards	6	239	197,500	1.2
Southern Leewards	4	74	39,600	1.9
Total	27	2,221	1,170,550	1.9

TABLE 5

Stages in the breeding cycle of frigatebirds on Caroline Atoll,
21–29 September 1988.

Species	Nest stage/Approximate age in days from laying					
	Juv.	Primaries	Scaps.	Downy	Naked	Eggs
Great	191-220	101-190	81-100	(56-80) ^a	(56-80) ^a	0-55
Lesser	181-210	91-180	71-90	56-70	46-55	0-45
Species	No. nests in each stage					
	Juv.	Primaries	Scaps.	Downy	Naked	Eggs
Great	22	46	27	(30 ^a)		19
Lesser	4	13	4	5	0	0

^a Duration of naked and downy chick stages are lumped because it was often impossible to see into canopy nests.

TABLE 6

Sooty tern colonies on Caroline Atoll, 27–28 September 1988.

Colony Location	Area	Calculated Population (Mean Pairs ± SE)	Nest Stage	Approx. Weeks From Laying
Long Island, A	44,100 m ²	127,449 ± 30,429	hatching eggs, downy chicks	4-5
Long Island, 1 N	24,200 m ²	41,382 ± 5,808	chicks with short tails, juv. plumage	7-10
Long Island, 1 S	6,400 m ²	10,944 ± 1,536	“	7-10
Bo'sun Bird Islet, old	3,375 m ²	6,883 ± 1,575	fledglings	11-12
new	3,375 m ²	1,538 ± 758	new eggs	1-2
Total	75,075 m ²	188,196 ± 40,106		

TABLE 7

Density of white terns on occupied islets by islet group, Caroline
Atoll, September 1988.

Islet Group	# Islets	Vegetated Area (ha)	# White tern Pairs	Density (pairs/ 1,000 m ²)
Nake	1	66.63	1,094	1.64
Long	1	49.60	751	1.51
South	1	86.10	381	0.43
Windward Islets	9	36.09	1,164	3.23
South Nake Islets	6	8.50	122	1.44
Central Leeward Islets	9	33.56	408	1.22
Southern Leeward Islets	4	6.47	37	0.57
All Occupied Islets	31	286.88	3,957	1.38

TABLE 8

Lizards collected on Caroline Atoll, 1965–1988.

Species	Specimens:	
	Clapp & Sibley 1971a	Present Study
Mourning gecko <i>Lepidodactylus lugubris</i>	USNM 158355-57	USNM 299773
Polynesian gecko <i>Gehyra oceanica</i>	USNM 158353-54	--
Snake-eyed skink <i>Cryptoblepharus poecilopleurus</i>	--	USNM 299772
Moth skink <i>Lipinia noctua</i> ^a	USNM 158358	
	--	USNM 299768-70
<i>Emoia impar</i>		
Azure-tailed skink <i>Emoia cyanura</i>	--	USNM 299771

^a USNM 158358 has recently been reidentified by R.I. Crombie as *Lipinia noctua*, not *Emoia nigra*, as reported in Clapp & Sibley (1971a).

TABLE 9

Comparative abundance of Caroline's breeding seabirds in the Line Group.

Species	Estimated Population	Comparative Abundance in the Line Group
Red-tailed tropicbird	300 ^a	Second largest population
Masked booby	400	Fourth largest population
Brown booby	40	Third largest population
Red-footed booby	7,000	Third largest population
Great frigatebird	6,100	Third largest population
Lesser frigatebird	200+	--
Sooty tern	912,000	Third largest population
Brown noddy	3,000	Third largest population
Black noddy	17,000	Largest population (largest in Kiribati)
Blue-gray noddy	<10	--
White tern	8,000	Largest population (largest in Kiribati)

^a Based upon nest count in 1990.

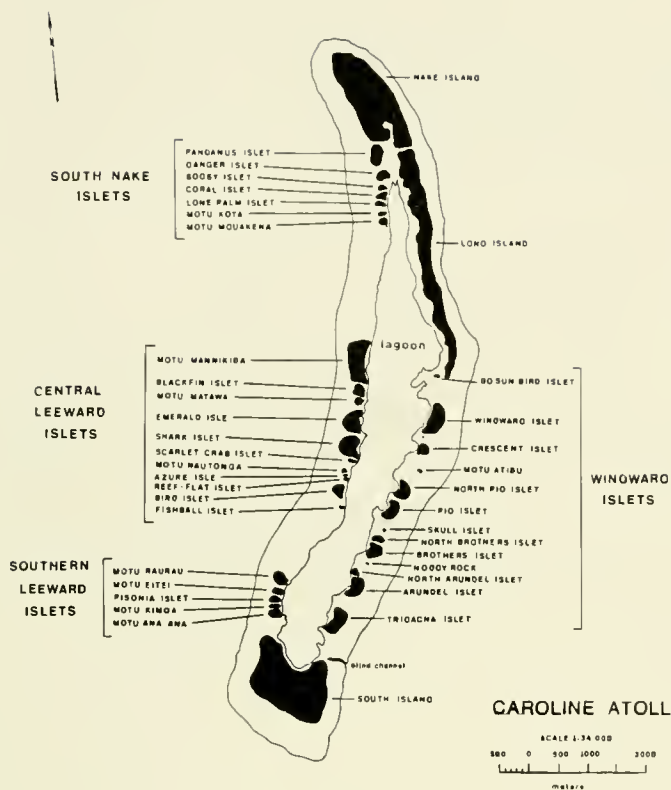


Fig. 1. Caroline Atoll, Republic of Kiribati, with newly-named islets.

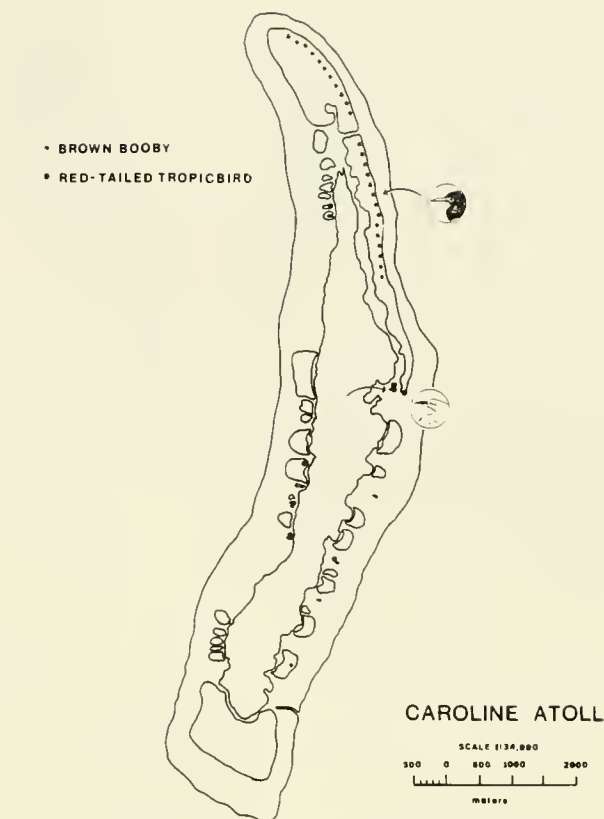


Fig. 2. Distribution map of breeding red-tailed tropicbirds and brown boobies on Caroline Atoll, September 1988. In this and the following distribution maps, arrows indicate concentrations of breeding birds.

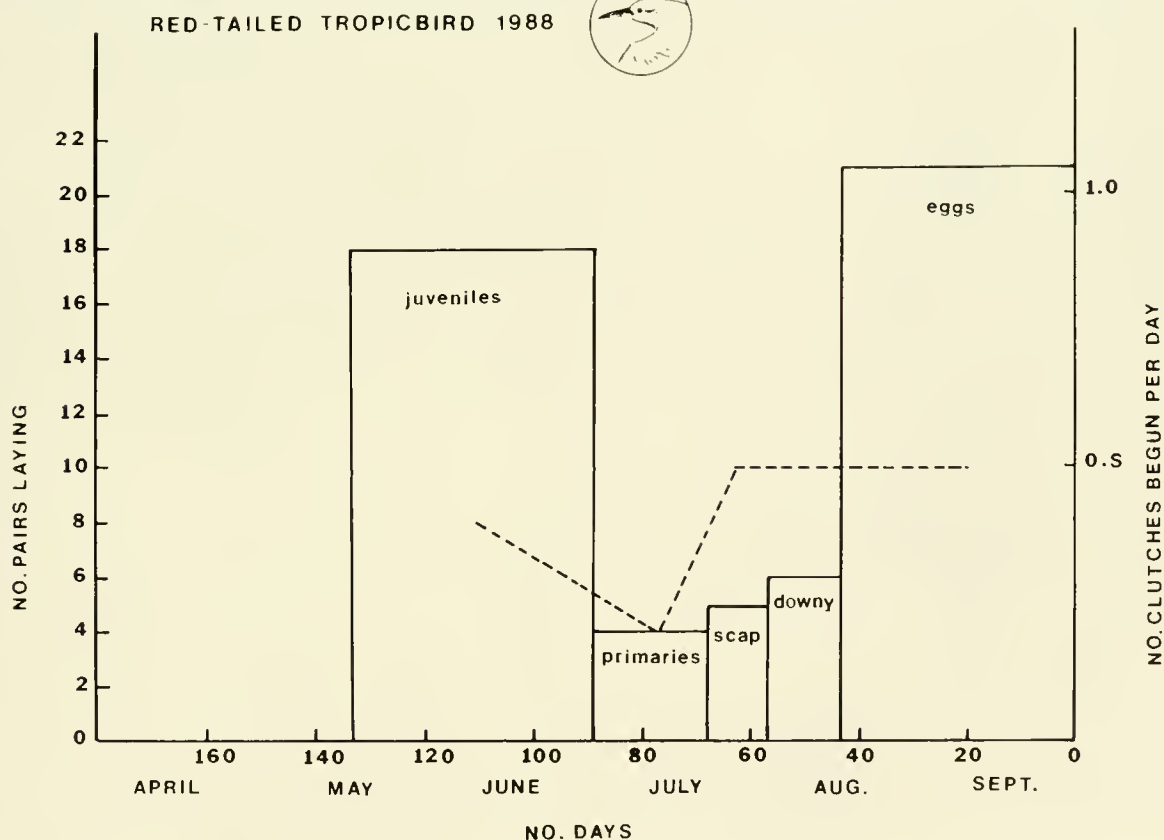


Fig. 3. Approximate laying dates for red-tailed tropicbird nests found on Caroline Atoll in September 1988. In this and the following similar figures the numbers of nests begun during a given time period (bars) were determined by tallying each nest into one of several age classes (bar labels); bar widths indicate length in days for each class. The dotted line connects mean number of surviving clutches begun per day for each class. For example, a juvenile found in September began its egg stage in the previous May or June. The number of days are counted backwards from field observations.

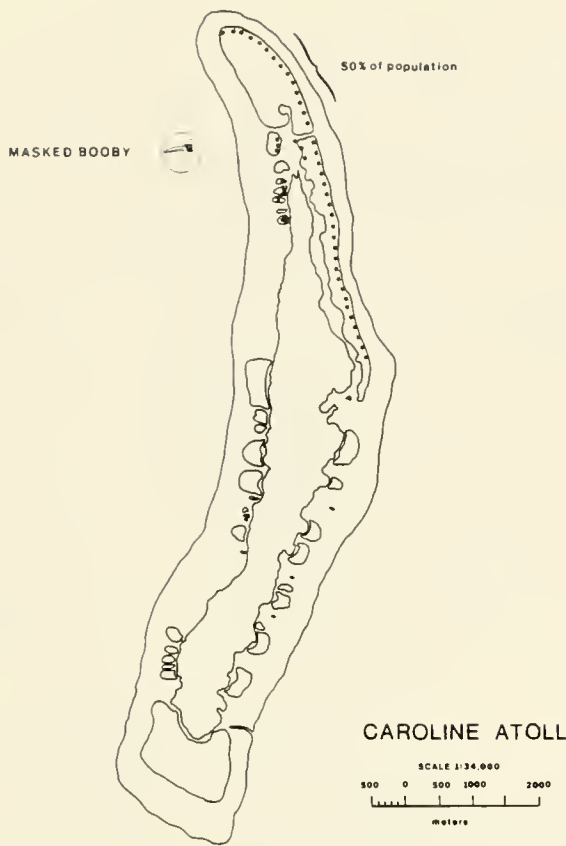


Fig. 4. Distribution map of breeding masked boobies on Caroline Atoll, September 1988.

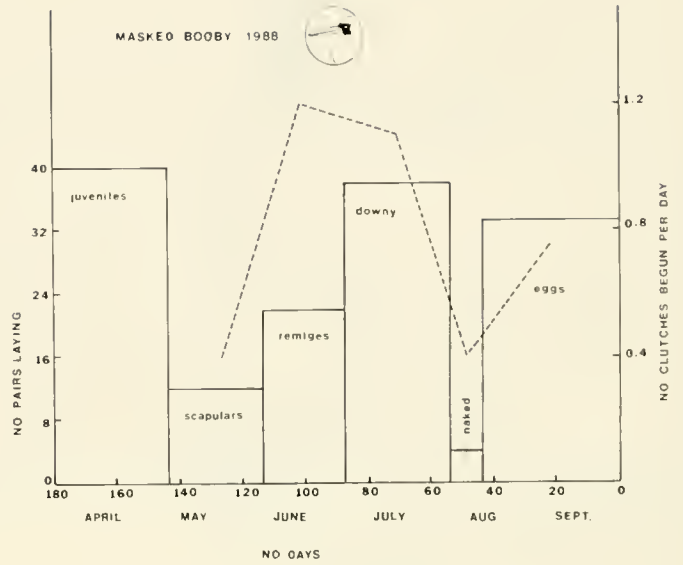


Fig. 5. Approximate laying dates for masked booby nests found on Caroline Atoll in September 1988.

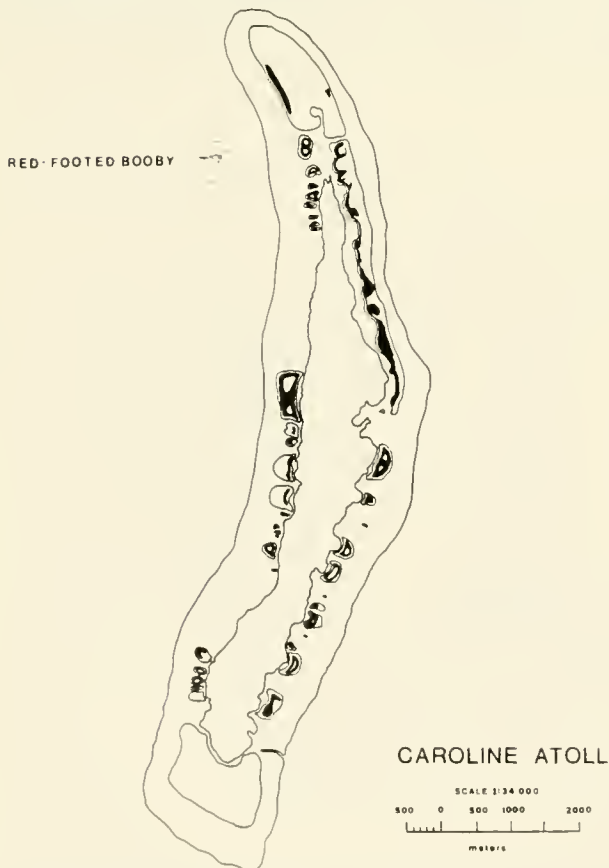


Fig. 6. Distribution map of breeding red-footed boobies on Caroline Atoll, September 1988.

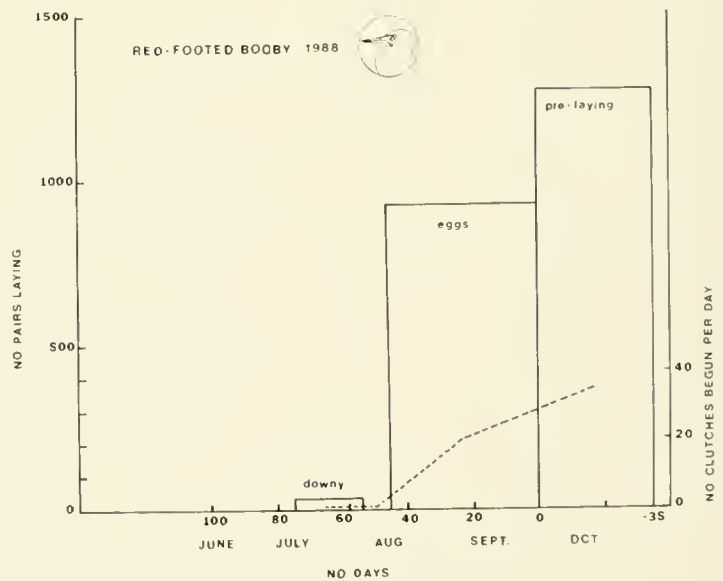


Fig. 7. Approximate laying dates for red-footed booby nests found on Caroline Atoll in September 1988.



Fig. 8. Distribution map of breeding great and lesser frigatebirds on Caroline Atoll, September 1988.

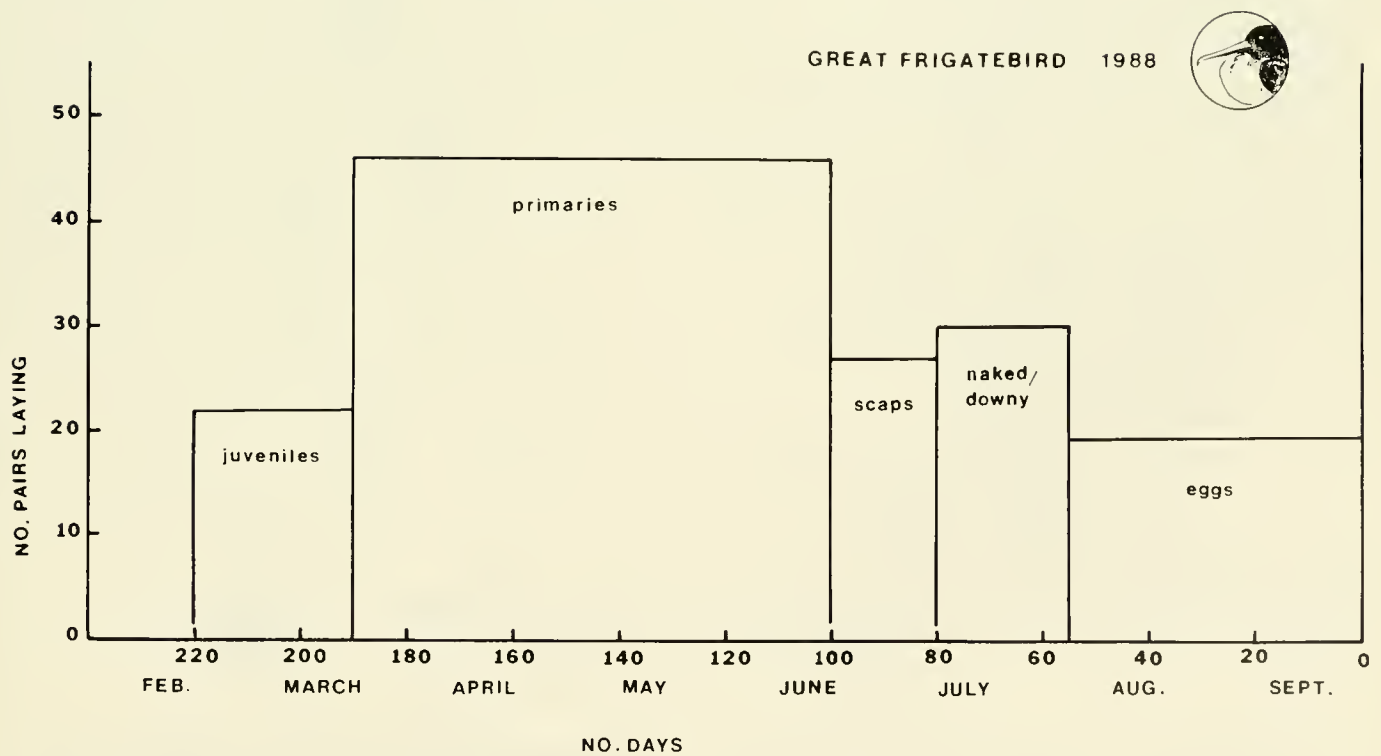


Fig. 9. Approximate laying dates for great frigatebird nests found on Caroline Atoll in September 1988. See Figure 3 for explanation.

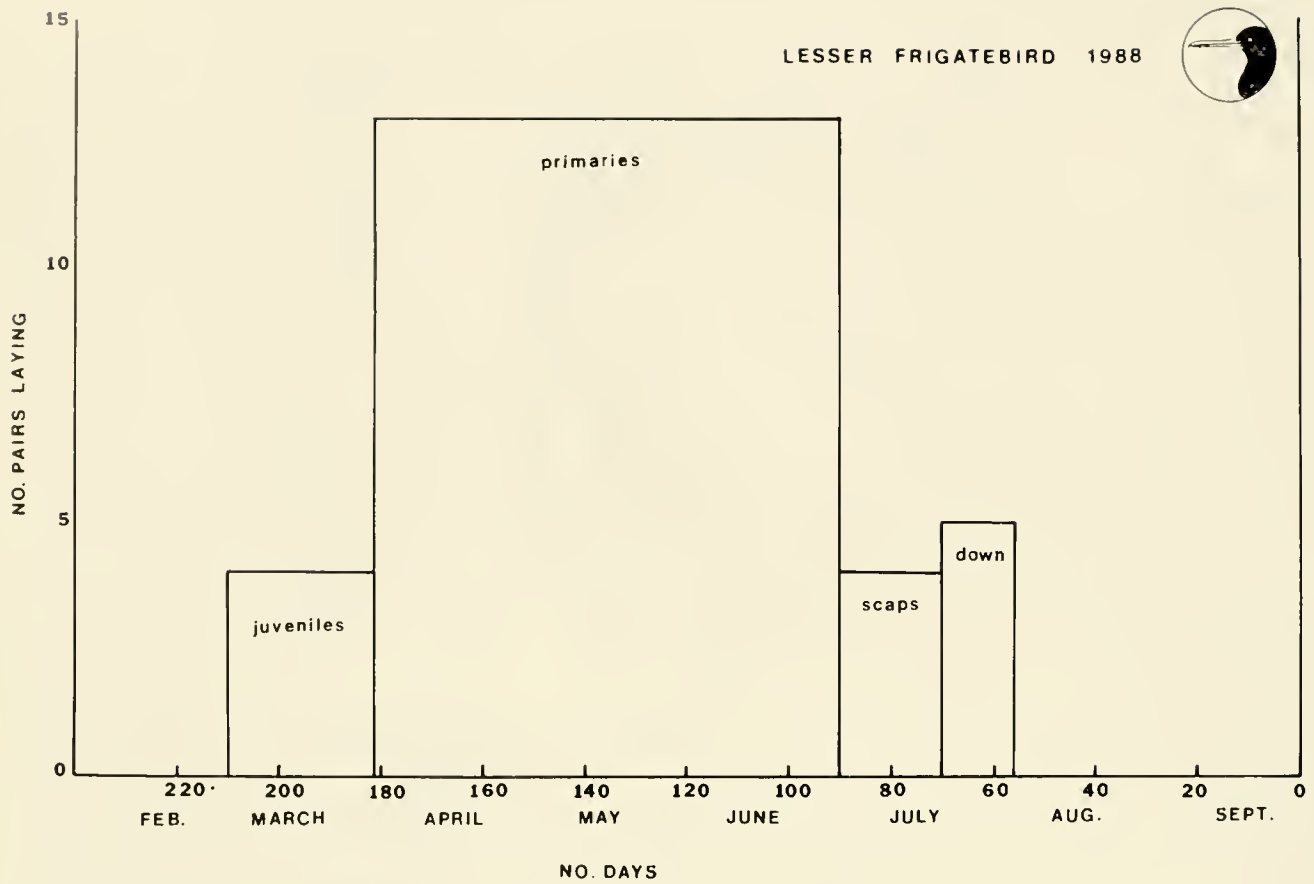


Fig. 10. Approximate laying dates for lesser frigatebird nests found on Caroline Atoll in September 1988.

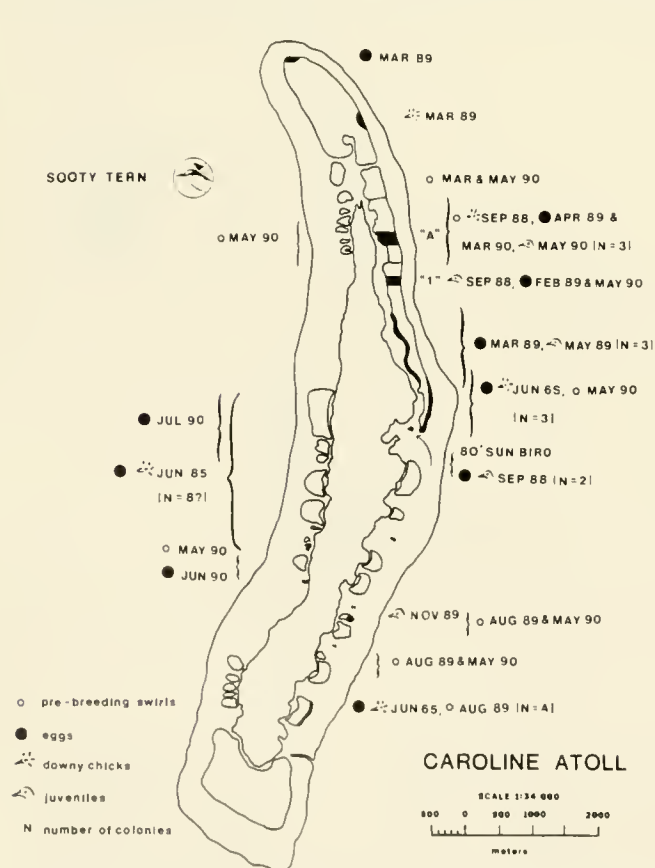


Fig. 11. Distribution map of breeding sooty terns on Caroline Atoll, September 1988–July 1990..

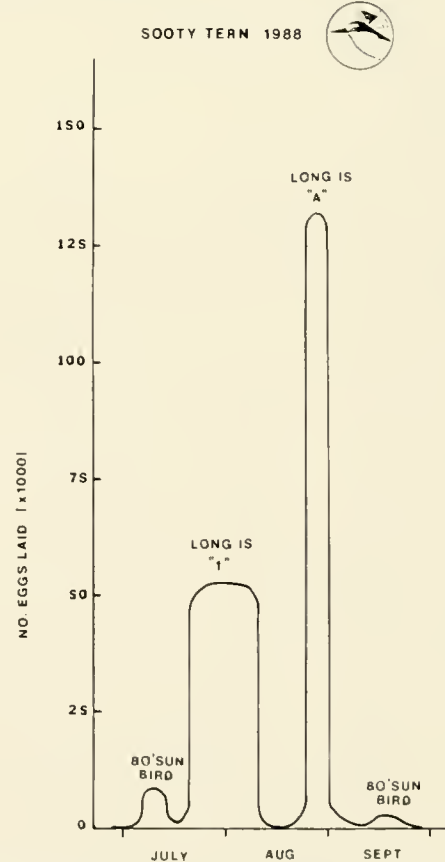


Fig. 12. Approximate laying dates for sooty tern young found on Caroline Atoll in September 1988. See Figure 3 for explanation.



Fig. 13. Distribution map of breeding brown noddies on Caroline Atoll, September 1988.



Fig. 14. Distribution map of breeding black noddies on Caroline Atoll, September 1988.



Fig. 15. Distribution map of breeding white terns on Caroline Atoll, September 1988.

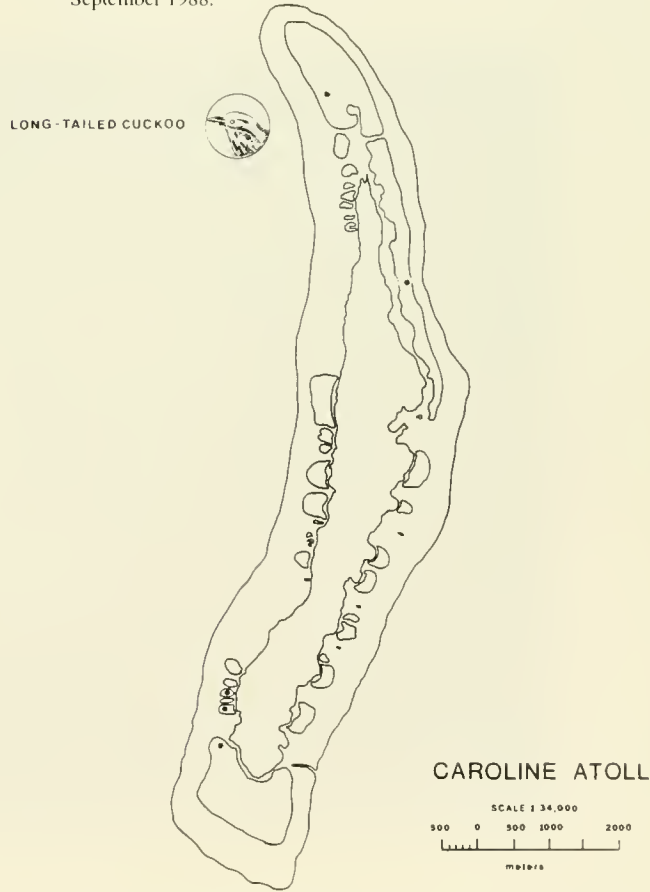


Fig. 16. Tentative distribution map of the long-tailed cuckoo on Caroline Atoll. The species most likely utilizes all well-wooded islets.

SEABIRD BREEDING
SPECIES DIVERSITY



Fig. 17. Seabird breeding species diversity by islet, Caroline Atoll.

COCONUT CRAB

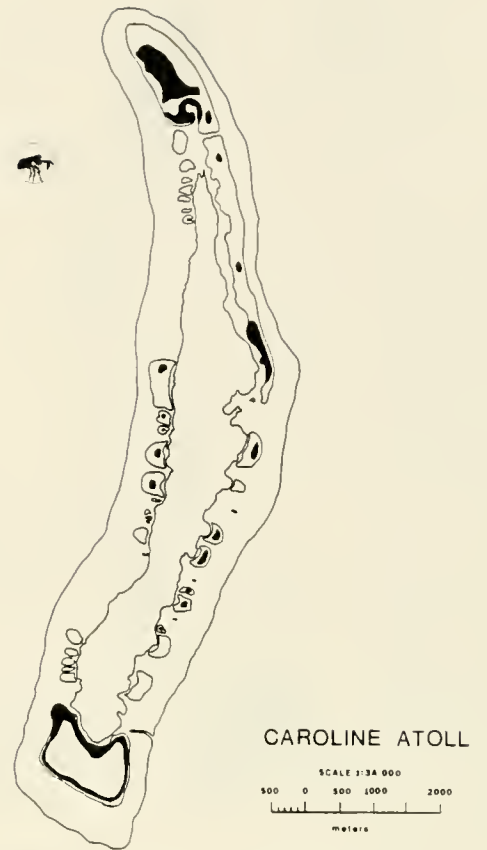


Fig. 18. Distribution map of coconut crabs on Caroline Atoll.



Pl. 1. Incubating red-tailed tropicbird, Bo'sun Bird Islet, Caroline Atoll, 25 September 1988. The nest scrape is in fine coral rubble under a *Tournefortia* shrub.



Pl. 2. Masked booby adult with egg on coarse coral rubble substrate with *Portulaca* mat, Nake Island, Caroline Atoll, 26 September 1988.



Pl. 3. White tern adult with egg in typical nest site, a dead *Tournefortia* branch, South Island, Caroline Atoll, 23 September 1988.

1.3 First Records of the Long-tailed Cuckoo (*Eudynamis taitensis*) on Caroline Atoll, Southern Line Islands, Republic of Kiribati

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Introduction

The long-tailed cuckoo (*Eudynamis taitensis*) performs what is perhaps the most remarkable overwater migration of any land bird (Lack, 1959). It breeds in New Zealand and is known to winter in the islands of the central Pacific Ocean, with stragglers seen as far as Palau to the west and Pitcairn to the east (Bogert, 1937). Although the Line Islands are along the northeastern perimeter of this range, the cuckoo has never been reported for the Line or Phoenix Islands (Pratt *et al.*, 1987). In 1883, when Dixon (1884) visited Caroline Atoll (10°S, 150°W) at the southeastern end of the Line Islands, he reported that a colleague had heard "the notes of a singing bird," but no land bird was collected. In June 1965, biologists from the Pacific Ocean Biological Survey Program visited Caroline Atoll but failed to detect land birds (Clapp & Sibley, 1971).

We encountered the long-tailed cuckoo on four islets during our 22–29 September 1988 survey of all 39 islets of Caroline Atoll as part of a research team from the Soviet oceanographic research vessel *Akademik Korolev*. Harsh monosyllabic or disyllabic call notes, presumably of this species, were first heard on three islets: South, Pisonia, and Long (see Kepler *et al.*, Subchapter 1.1, this volume, for islet locations). Then, on 25 September, a single bird, probably of this species, was heard and briefly seen on South Island. On 26 September, an individual was positively identified (CBK; ca. 25 m; ×10 binoculars) on Nake Island.

In an attempt to capture this species, or any other undiscovered land bird, we operated mist nets at three locations on the atoll. In 14.5 net hours (daylight hours only; ATX 4-shelf nets, 2.6 × 12 m; mesh size 36 mm) beneath a 10–15 m *Cocos* canopy on South Island, only a single bristle-thighed curlew (*Numenius tahitiensis*) was captured. On Long Island two nets along a *Pisonia*–*Cocos* interface (canopy at 6–8 m) were unsuccessful in 27.5 net hours. Finally, on 28 September

we collected a male long-tailed cuckoo on Long (US National Museum No. 607191) in 1.5 net hours along a *Pisonia*–*Tournefortia/Cordia* interface with a short canopy (4–6 m) where two of us (AKK, KT) had heard and followed a cuckoo-sized land bird for about 20 minutes the day before.

The following measurements of the specimen were taken immediately after collection: mass 125 g, length 411 mm (central rectrices still growing so measurement was to the tip of the worn rectrices adjacent to central rectrices), culmen 25.4 mm, and wing chord 179 mm. Soft part colors within 30 minutes of death, compared with Smithe's (1975) color key, were ridge of bill, No. 219 Sepia; lateral margin of bill, No. 86 Pale Neutral Gray; lower mandible, No. 53 Buff-yellow; iris, No. 124 Buff; foot pad, No. 153 Trogon Yellow; and dorsal surface of foot and tarsus, No. 150 Bunting Green.

These records establish the long-tailed cuckoo as a winter visitor to the Line Islands. Since our 1988 visit, we learned from correspondence and personal discussions with the atoll's only human inhabitants and wardens, Ronald and Anne Falconer, that cuckoos occasionally occurred in April, 1989, near their dwelling on Motu Ana-Ana, the southernmost leeward islet. This was confirmed by AKK with further sightings on two subsequent trips to Caroline in March and May 1990 (Kepler, 1990). Our original observations at five widely scattered locations (the most distant were 9 km apart) suggested that several individuals were present on the atoll during our visit. Subsequent observations suggest that this species disperses regularly to Caroline Atoll and perhaps some others of the better-vegetated Line and Phoenix Islands as well.

We are pleased to thank Mr. Harold J. O'Connor and Mr. Steve Kohl (US Fish & Wildlife Service) and Professor Alla V. Tsyban (Goskomgidromet, USSR) for organizing the Third Joint US–USSR Bering & Chukchi Seas Expedition that made these observations possible.

1.4 A Study of the Benthic Communities of Caroline Atoll (Line Islands, Pacific Ocean)

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Introduction

The study of coral atolls, which constitute one of the most highly productive biological systems in oligotrophic tropical waters, is of considerable theoretical and practical value. On one hand, rapid human population growth over the past few decades, with the concomitant shortage of protein-rich foods, has driven a never-ending search for new protein sources. The study of coral reefs as highly productive biological systems would be helpful for establishing marine farming facilities. On the other hand, burgeoning industrialization and the increasingly intensive use of all natural systems has caused considerable damage to coral reefs (Gomez & Yap, 1985). There is, therefore, an urgent need for coral reef monitoring. Uninhabited Caroline Atoll, situated far from principal sea routes, would be considered an excellent monitoring site. With this in mind, we spent a week studying the status of the coral reefs and surveying the benthic communities around South Island and the Southern Leeward Islands (Kepler *et al.*, Subchapter 1.1, this volume) in Caroline Atoll (Fig. 1). Regrettably, time constraints did not permit a study of sufficient scope and depth. The present paper is therefore limited to a general description of benthos distribution in the accessible portions of the reef and to an account of a uniquely interesting reef situated within the atoll lagoon.

At low tide, the Caroline Atoll Lagoon is linked to the ocean by shallow passes of no greater than 0.5 m in depth. Several narrow intralagoonal reefs subdivide the central lagoon at low tide. The depth of the lagoon does not exceed 10 m. The largely sandy bottom includes isolated patches of fragile coral colonies, mostly *Acropora*.

With few exceptions, the outer side of the reef near the southern islands has the classical structure of most coral reefs (Preobrazhenskiy, 1986). The narrow shallow-water lagoon facing the islands gradually becomes a reef flat cemented by encrusted calcareous algae. This is rather extensive, averaging 562 m; range 396–759, $N = 100$ sites (Kepler *et al.*, Subchapter 1.1, this volume). The reef flat is surmounted by widely spread limestone coral knolls or "coral heads." Further seaward, the reef flat, with the usual channels and overhanging ledges, breaks off. At a depth of 5–6 m it becomes a buttress zone (i.e., a radically crosscut sloping terrace consisting of individual spurs or benches that become narrower in the oceanward direction). It is the latter zone that constitutes the main portion of the reef, with its abundant growth of corals (*Acropora*, *Pocillopora*, etc.). It is this growth that accounts for the origin and continued development of the reef and the entire coral atoll. It was the status of the coral settlements in the



Fig. 1. Location of the *Acropora-Tridacna* reef and of hydrobiological section I-I of Caroline Atoll.

buttress zone that afforded an indication of the "health" of the reef. Our studies showed that not less than 50% of the surface area of the outer slope of the Caroline Atoll reef was covered by living coral colonies. Assessment on this basis, using the method of cross sections and areas (Gomez & Yap, 1985), showed the condition of the reef to be sound. The notorious "crown of thorns" starfish (*Acanthaster planci*), responsible for the devastation of reefs in other parts of the Pacific Ocean, was seen only once.

The littoral zone of the lagoon facing South Island was sandy. The sand was filled with holes made by burrowing Polychaeta and Balanglossi. Also present, sometimes in clusters, were the mollusks *Cerithium columna* and *Cerithium* sp., a few *Calappa* sp. crabs, and gastropod mollusks *Melarchape undulata* and *Nerita plicata*, the latter settling by water's edge on trees whose branches dip all the way down to the water.

The northeastern side of South Island was washed by strong oceanic surf throughout our stay at the atoll. The prevailing wind in this area is easterly (see Kepler *et al.*, Subchapter 1.1, Appendix 2, this volume), an observation that is consistent with the presence on the eastern side of South Island of extensive coarsely fragmented coral limestone banks 2–2.5 m high, attributable to windstorms. These storm banks contained large numbers of fresh bivalve mollusk (*Asaphis* cf. *violascens*) shells, providing evidence for a large population of these burrowing animals. The shallow islandward lagoon and reef flat, with its extensive sand lenses, is inhabited by the aforementioned bivalves, large numbers of gastropods of the genera *Cerithium*, *Drupa*, *Cypraea*, et cetera, as well as by predatory mollusks of the genus *Conus*, including unusually large specimens of *Conus ebreus* (up to 55 mm long).

The coral reef on the western side of South Island received closer scrutiny. The distribution of organisms over the hydrobiological section (I-I) is indicated in Fig. 2.

The beach of the island showed many large red hermit land crabs *Coenobita perlata*, as well as *Ocypode* sp. crabs. Next to the beach lay a zone of lifeless coral limestone remarkable for its extreme lack of living organisms during the season of the year when we visited. This zone became very narrow to the south. The fact that the sea had until recently extended this far was evidenced only by small numbers of *Melastapha undulata* clinging to the underside of sun-baked coral slabs. It appears that when the wind direction changes to westerly, powerful surf inundates this area during high tide. During our visit, however, surf continued to crash against the opposite side of the atoll. The dry, lifeless zone ended with a ledge approximately 1 m in height. The water reached this ledge during high tides. The dominant fauna consisted of small hermit crabs, *Grapsus* sp. crabs, holothuria, and the mollusks *Nerita plicata* and *Thais*

armigera. Further seaward, the stones in the never-drying pools of the islandward part of the lagoon harbored the following fauna: *Diadema* sp. urchins; the mollusks *Cypraea moneta*, *Cerithium columna*, *Cerithium* sp., *Vasum tubiferum*, *Conus ebreus*, and *Conus sponsalis*; the crabs *Eriphia* sp. and *Actaea* sp.; three species of sea cucumbers (Holothuroidea); *Linckia* sp. starfishes; and black and grey brittle stars (Ophiuroidea). Part of the coral limestone in the same area was encrusted with the calcareous algae *Porolithon* sp. and *Lithothamnion* sp. To seaward, the littoral pools became deeper and somewhat larger, interdigitating to form the islandward lagoon. The bottom in this area consisted of coral limestone with small patches of coral fragments and sand. The bottom was strewn with limestone knolls that resulted from the intense buildup of calcareous algae and corals of the genera *Porites*, *Pocillopora*, *Acropora*, and *Montipora*. These limestone knolls were cavernous and often caved in under the weight of an adult human. The fissures and caverns contained numerous small crabs and other crustaceans, as well as sponges. Also prevalent were algae bushes (*Halimeda* sp.).

The bottom sloped upward towards the tidal strip, where it was succeeded by a highly tenacious, firmly attached fauna of a very particular kind. Unfortunately, because our examination was confined to the upper portion of the reef flat, the richly populated interior portion remained unstudied. The cavities and fissures of the top portion of the reef flat revealed an abundance of corals of the aforementioned genera. Dead coral colonies, as well as all of the old coral limestone formations, were densely encrusted with calcareous algae that cemented the reef-flat surface together. There were many gastropods (large *Turbo argyrostomus* and the smaller *Drupa ricina*, *D. morum*, *D. grossularia*, etc.) as well as large orange-colored hermit crabs. The perpetually surf-washed tidal areas at the

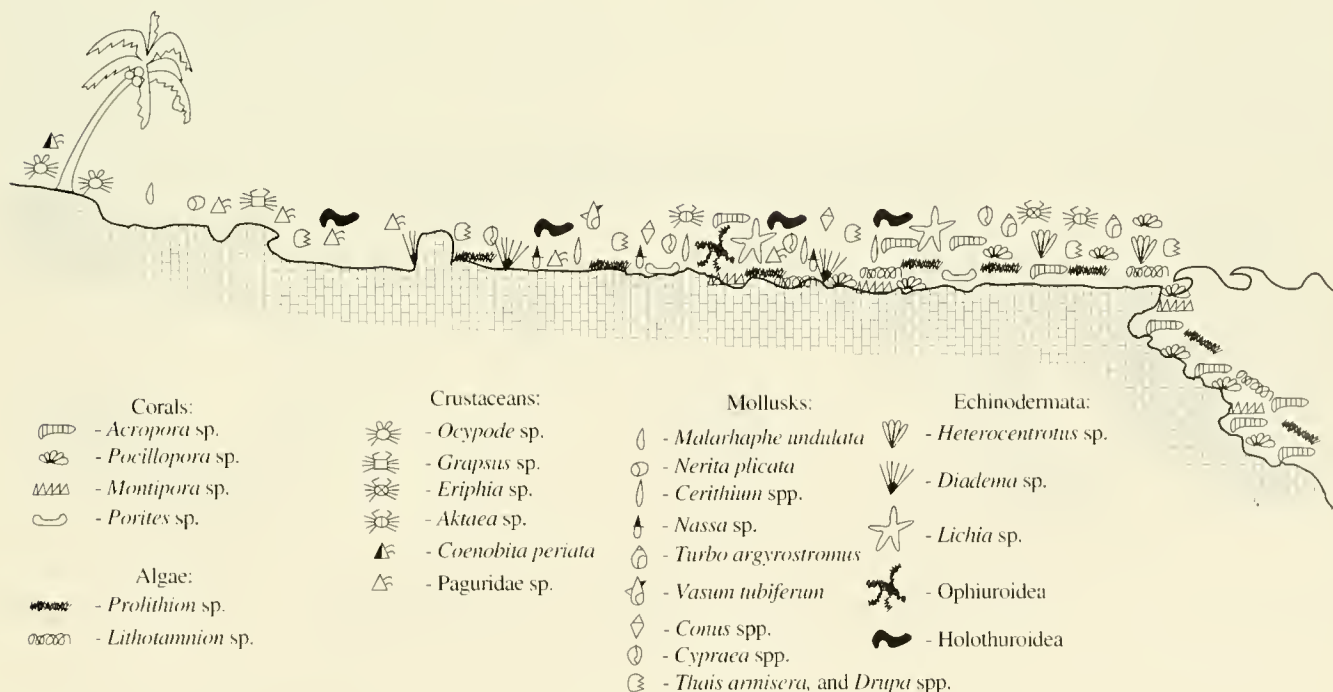


Fig. 2. Distribution of organisms on the reef on the western side of South Island of Caroline Atoll (Section I-I).

very edge of the flat exhibited magnificent specimens of the sea urchin (*Heterocentrotus* sp.), with spines as thick as eigers. The limestone caverns sheltered smaller crabs (*Eriphia* sp. and *Actaea* sp.). The edge of the reef flat dropped abruptly some 5–6 m, in places forming an overhanging ledge that overlooked the most abundantly populated and significant portion of the reef, namely the buttress zone with its rich variety of coral species.

Caroline's lagoon enclosed a unique natural structure, an unusual *Acropora*–*Tridacna* reef (Fig. 1, Chapter Frontispiece). This reef extended from the southernmost islet (Ana-Ana) in the Southern Leeward Islands into the interior of a shallow lagoon. In the middle of the lagoon, it divided into two branches: a northern branch that ended in the center of the lagoon, and an eastern branch that extended all the way to the opposite shore. The reef, in effect, partitions the lagoon into two parts; a wide channel had to be dug to permit a small flat-bottomed rubber boat to pass. The width of the reef varied from 15 to 20 m, attaining 30 m at its fork. Most of the reef surface stood above sea level, with many of the *Tridacna maxima* and corals partially drying out during very low ebb tides.

The distribution of organisms over a typical cross section of the reef is shown in Fig. 3. Five distinct zones (two edges, two lateral strips, and a central strip) were clearly evident.

The edge strips, populated mostly by fragile colonies of *Acropora secale*, *A. palmerae*, and *Acropora* sp., are growth zones where vital activity keeps increasing the reef's width. The dominant corals of the genus *Acropora* completely cover the steep slopes of the reef as well as the neighboring rudimentary reefs that do not reach the surface of the water in the lagoon. The lush coral growth resembles a huge domed topiary.

The thickness of the living coral layer ranges from 20 to 70 cm. Parts of the reef slope exhibited scarps that probably formed as a result of the collapse of fragile coral colonies unable to carry their own weight. It is at these scarps that measurements were made of the longest coral branches, some of which were found to attain a length of 70 cm. The spaces between the fine coral tentacles of the reef slope were filled with beaded (moniliform) algae (*Halimeda* sp.). Also evident at the base of the reef slope were a few, mostly large, specimens of *Tridacna maxima*. Beginning at a depth of 5 m and extending to the reef base were sparse, isolated growths of fungiform coral (*Fungia granulosa*). The colonies of *Acropora* were fine and fairly fragile, as is typical in the still-water portions of many lagoons. It was risky to approach the edge of the reef, since the loose and brittle coral colonies tended to crumble underfoot.

Beyond the edge zones (including the reef slopes, and extending several tens of centimeters into the reef flat) lie lateral zones where *Tridacna maxima* clams are especially abundant. These lateral zones have a width of 3–5 m on either side of the reef (Fig. 3). Particularly striking was the very high density of *Tridacna*, firmly attached to the reef surface by the byssus, which formed veritable bunches atypical for these large mollusks in other regions. Not uncommon were bunches of five or six clams attached to one another by the byssus. The average shell length for *Tridacna* found atop the reef was 12–13 cm, with a maximum length of 19–20 cm for individual specimens. No less striking was the variety of coloration exhibited in their mantles, probably occasioned by the presence of symbiotic algae. We were able to identify as many as 10 shades of blue, green, and light brown pigmentation. The average *Tridacna* population density in the lateral zone

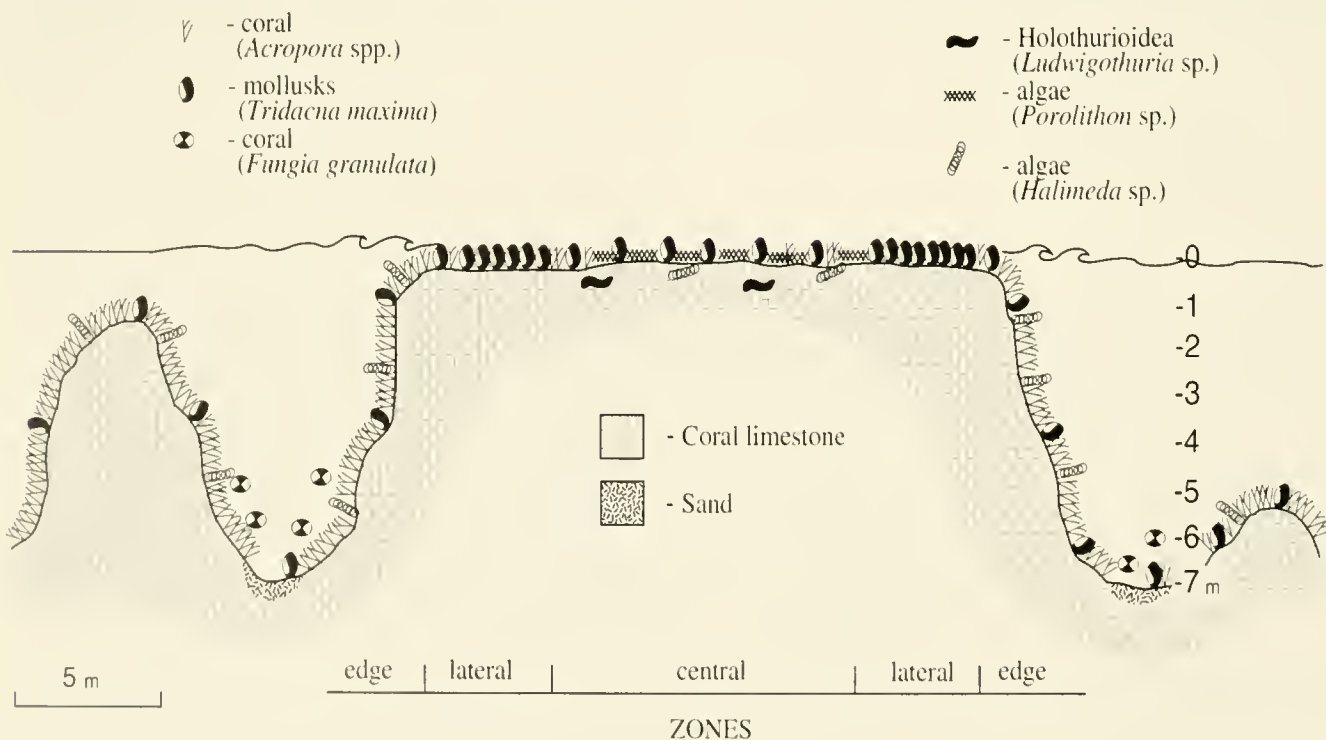


Fig. 3. Cross section of the *Acropora*–*Tridacna* reef in the lagoon of Caroline Atoll.

was estimated at 35 living individuals/m², with some 0.25-m² patches containing as many as 20 of these mollusks. In addition to *Tridacna* clams, the lateral strips included small colonies of *Acropora* sp. coral and some less abundant lamellate *Montipora* sp. Also present were algae (*Halimeda* sp.) occupying spaces between *Tridacna* shells and coral colonies, as well as calcareous fouling algae encrusting the mollusk shells and dead portions of coral colonies.

A central strip 7–10 m in width accounts for most of the reef flat. This site harbored most of the dead coral colonies and empty *Tridacna* shells, firmly bonded to the reef surface by calcareous fouling algae (*Porolithon* sp.). Nearly 80% of the surface area of the central strip was covered by these algae, which gave the middle portion of the reef added strength. The live *Tridacna* population density in this strip was one order of magnitude lower (an average of 4–5 individuals/m²) than in the lateral strips. The strip also contained widely scattered colonies of *Acropora* sp. and, more commonly, bluish scales of *Montipora* sp. coral colonies, including small clumps of *Halimeda* sp. Another denizen of the central strip is the holothurian *Ludwigothuria* sp. (approximately 1 specimen/m²).

The central and lateral strips exhibited a few small holes 4–8 cm in diameter surrounded by empty shells of smaller, thoroughly consumed *Tridacna*. These were probably the remains of meals taken by predators, namely small octopuses that are able to open bivalve shells without damaging them. The typical division of the reef into the aforementioned zones is disrupted in some places. In these instances, the central strip of the reef contained a shallow depression of friable structure populated by corals and *Tridacna*, with small amounts of calcareous fouling algae. This is probably an intermediate stage in the merging of individual smaller reefs with the larger reef traversing the entire lagoon. One such smaller and still-growing reef is shown on the left side of the reef cross section in Fig. 3.

It is interesting to note that the *Acropora–Tridacna* reef is a natural farm producing large bivalves of commercial value. The efficiency of the “farm” is difficult to assess without data on its productivity. However, a count of the *Tridacna* present is possible. According to the most conservative estimates, the surface of the *Acropora–Tridacna* reef, extending 1 km into the

lagoon of Caroline Atoll, contains approximately 300,000 *Tridacna* clams, the raw weight of their flesh equaling not less than 30 tons. It should be noted that the *Acropora–Tridacna* reef actually investigated was not the only one in the lagoon (Chapter Frontispiece; Kepler *et al.*, Subchapter 1.1, this volume, Figs. 47, 48, 57). There were, in fact, several such reefs, and if we assume that they are of similar structure, the above figures can be multiplied by an appropriate factor to show the actual reserves of valuable food protein available in Caroline’s waters.

The unusually high density of living *Tridacna* in Caroline’s lagoon was especially striking, exceeding any previously known populations of both *Tridacna maxima* and *T. crocea* (usually more abundant in other parts of the World Ocean). For example, the Palau Islands (western Pacific) were reported to have just six *T. maxima* and 153 *T. crocea* within an area of 1,100 m² (Hardy & Hardy, 1969), whereas the same area on the *Acropora–Tridacna* reef in Caroline Atoll lagoon contained 16,500 *T. maxima*. Richards (1985) found that *T. maxima* in the Tuamotus numbered 6–20/m² at Takapoto Atoll, and up to 60/m² at Reao Atoll. Although these are the highest densities previously reported, they do not equal the numbers found in the densest patches on Caroline.

The very considerable effect of such an enormous mass of large mollusks on the entire atoll is also noteworthy. This is because in symbiosis with zooxanthellae, which are the principal food of the *Tridacna* clam, the latter experience intensive growth and in turn enrich their habitat with proteins (Ricard & Salvat, 1977). Data concerning the natural *Acropora–Tridacna* reef could be put to use in creating artificial reefs in other parts of the ocean to achieve considerably enhanced productivity.

The sound condition of the coral reef around Caroline Atoll, as well as the presence in its lagoon of a uniquely interesting natural feature in the form of the *Acropora–Tridacna* reef, may be deemed sufficient grounds for organizing a marine reserve in the area.

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Chapter 2:

INVESTIGATIONS AND ANTHROPOGENIC ECOLOGY

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2.1 Distribution of Chlorinated Hydrocarbons in Ecosystems of the Equatorial Pacific

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Introduction

It is a well-known fact that chlorinated hydrocarbon pesticides (CHP's), which earned their developers a Nobel Prize, have been both a great benefit to mankind by making it possible to rescue up to one-half of the world's cereal-grain harvests from pests and a detriment to the environment by their trait of extreme stability causing them to build up in the environment. In just a few years, their environmental hazard has become apparent.

The multiplicity of pathways and the high rates of CHP transport led to a situation whereby in the early 1970's they had accumulated on a worldwide scale, being detectable in virtually all environments, including mountain-peak glaciers and deep-ocean depressions. Later, the world was to see a no less extensive buildup of other classes of chlorinated hydrocarbons (CH's), namely polychlorinated biphenyls (PCB's), chlorinated terpenes, dioxins, benzofurans, et cetera, which were being used not only in agriculture but also in various industries and even in health care fields.

Despite the fact that most industrialized countries had invoked total or partial bans upon the use of CH's in open-cycle processes, their production on a global scale remains almost undiminished, since no effective alternative for protecting agricultural harvests in tropical countries has yet been devised.

There is now a considerable body of scientific literature indicating that the World Ocean is the ultimate repository for CH's. According to the most reliable estimates (Tanabe, 1985), ocean waters are today the repository of as much as 70% of all the CH's ever released into the environment. Previous studies (Chernyak *et al.*, 1985b) showed that the rates of CH buildup and migration in constituents of the oceanic environment depend first and foremost on the physicochemical and hydrologic-geographic characteristics of various portions of the World Ocean. Hence, predictive estimates of increases in ocean pollution, which are bound to occur globally, require information on the forms and amounts of CH's present in various media and especially in little-studied regions such as the Pacific Ocean, where only a few expeditions have concerned themselves with CH's (Izrael & Tsyban, 1989). Our own recent studies (Chernyak & Mikhaleva, 1985a) were the first to include nearly *in situ* studies of microbial and photochemical PCB decomposition processes, which are the only processes presently at work to rid the oceanic environment of these xenobiotic substances. We were particularly interested in investigating PCB distribution at Caroline Atoll, a coral island remarkable for its diverse flora and fauna, where these CH's have accumulated, in markedly altered form and at a distance

of many thousands of kilometers from their sources. Their presence at these locations are probably occurring through atmospheric and oceanic transport.

The present paper sets out the findings and conclusions of comprehensive studies conducted in 1988 in the equatorial Pacific and at Caroline Atoll, which were obtained during the First Joint US-USSR Central Pacific Expedition aboard the R/V *Akademik Korolev*.

Materials and Methods

The locations of the sampling stations are shown in Fig. 1. The media sampled in order to establish the specifics of hydrochemical processes involving chlorinated hydrocarbons in background regions of the Pacific and coral-reef ecosystems were seawater, sediment, plankton, neuston, demersal organisms, and fishes. Specific studies conducted at Caroline Atoll also included corals, flora and fauna, and eggs of local bird species.

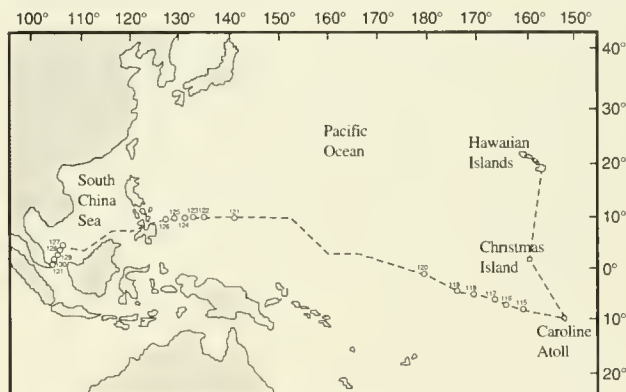


Fig.1. Expedition route and station locations in the Pacific Ocean and South China Sea (9 September to 31 October 1988).

Seawater samples, 100 l in volume, were filtered through XAD-2 resin at the rate of 20 l/h. The sorbed CH's were eluted with 80 ml of ethanol mixed with an equal volume of 2% sodium sulfate solution. The water-alcohol solution was doubly extracted with *n*-hexane (using 25 ml of hexane in each of the two extractions). The extracts were concentrated to a volume of 4–5 ml using a rotary evaporator, purified with concentrated sulfuric acid, neutralized with a 5% NaHCO₃ solution, rinsed twice, dried over sodium sulfate, and concentrated in a stream of pure nitrogen to a volume of 1 ml. The concentrate was injected into a Hewlett-Packard gas chromatograph with the aid of an autosampler. The chromatographic analysis conditions were as follows:

fused-quartz capillary column, length 30 m, and inside diameter of 0.32 mm; chromatographic phase DB-1 (0.25 μ m). The temperature program for the column was initial temperature, 120°C (1 min), rising to 250°C at the rate of 5°C/min. The chromatographic analysis time was 40 min, the injector temperature, 225°C, and the electron-capture detector temperature, 300°C.

The sediment samples were centrifuged for 20 min at a speed of 2,000 rpm to achieve total deposition of the silt. The residue was extracted with acetone, then doubly extracted with a 3:1 hexane-acetone mixture. The combined extract was washed by mixing with an equal volume of 2% sodium sulfate solution. The hexane layer was separated off, and the aqueous-acetone solution reextracted with additional hexane. The combined hexane extract was concentrated, then purified, first with sulfuric acid (to remove extracted organic compounds), then with tetrabutylammonium sulfate (to remove any sulfur compounds). The purified solution was concentrated down to 1 ml in a stream of pure nitrogen and chromatographically analyzed. The biological samples were crushed to obtain a homogeneous mass, defatted with acetone, then treated, following the procedure used, with sediment samples.

In order to investigate the effect of photochemical processes on the behavior of CH's in background ecosystems of the Pacific, experiments were conducted on the decomposition of a standard Aroclor 1232 solution in waters drawn from the equatorial Pacific and around Caroline Atoll under the action of sunlight.

The experiment was run in two 5-l reactor vessels, one exposed to sunlight, the other shielded using light-blocking foil. The surface area involved was 400 cm². The sterilized seawater in the reactors were spiked with an acetone solution of Aroclor 1232 to yield PCB concentrations in the water of 100 ng/l. The samples were extracted with *n*-hexane (twice, 50 ml each time), then concentrated to a volume of 2 ml in a rotary evaporator. They were then purified with concentrated sulfuric acid and chromatographically analyzed. Microbial degradation of the PCB under the same conditions was investigated for control purposes.

Results and Discussion

Data on CH levels in Pacific Ocean waters are presented in Tables 1 and 2.

Analysis of these results clearly demonstrated the dependence of the distribution of various PCB components on their molecular structure.

The distribution of hexachlorocyclohexane (HCH) is noteworthy since its total concentration was fairly high, though it was still several times lower than in the Bering and Chukchi Seas (Chernyak *et al.*, 1992), which are just as far removed from areas where this compound continues to be used. The composition of the HCH mixture (containing as much as 90% of the α -isomer) indicates that the sources of pollution are probably equatorial countries that employ vast amounts of technical-grade hexachloran on their crops. The relatively low

TABLE 1

Chlorinated hydrocarbon levels in the surface waters of the Pacific (ng/l).

Station Number	Chlorinated Hydrocarbon Levels				
	Total HCH	DDT	DDD	DDE	PCB
Caroline Atoll					
114	0.02	0.1	0.1	0.1	0.05
Caroline Atoll, lagoon					
L-1	0.01	1.0	0.5	0.3	0.02
L-2	0.01	0.8	0.3	0.3	0.01
L-3	0.01	1.0	0.3	0.5	0.02
L-4	0.01	1.1	0.3	0.3	0.02
Phoenix transect					
115	2.7	0.07	0.02	0.01	0.2
116	2.4	0.05	0.01	0.01	0.2
117	2.9	0.07	0.01	0.01	0.3
118	2.2	0.08	0.02	0.02	0.2
119	2.3	0.02	0.01	0.01	0.4
120	2.5	0.05	0.02	0.01	0.3
Marianas transect					
121	3.0	0.09	0.02	0.01	0.5
122	2.3	0.12	0.02	0.03	0.3
123	2.4	0.05	0.01	0.01	0.1
124	2.4	0.02	0.01	0.02	0.3
125	2.5	0.01	0.01	0.01	0.4
126	2.2	0.08	0.02	0.01	0.4
South China Sea					
127	4.2	0.18	0.04	0.02	0.3
128	4.5	0.10	0.02	0.03	0.4
129	4.8	0.10	0.04	0.05	0.3
130	3.7	0.22	0.10	0.03	0.3
131	3.3	0.18	0.05	0.05	0.3

TABLE 2

Distribution of chlorinated hydrocarbons over the water column in Pacific Ocean waters.

Depth (m)	Chlorinated Hydrocarbon Levels		
	Total HCH	DDT	PCB
Station 115			
0	2.7	0.10	0.2
10	2.5	0.08	0.2
100	2.0	0.05	0.2
1,000	1.7	0.01	0.2
Station 120			
0	2.5	0.08	0.3
10	2.3	0.08	0.3
100	2.1	0.04	0.2
1,000	1.8	0.04	0.2

hexachloran levels in the water here are likely due to their high volatility, which appears to be driving most of the HCH present in these hot climates into the atmospheric compartment.

The rather unusual distribution of HCH within the water column—that is, the marked drop in its level that occurs at considerable depths—is explained by the relatively high solubility of this pollutant in seawater and by the fact that it is present largely in dissolved form (in contrast to other globally-occurring CH's, which are largely sorbed and precipitate together with suspended matter). Hexachlorocyclohexane isomers are practically the only common pollutants whose behavior in the open ocean can be explained largely on the basis of hydrochemical factors.

Also worthy of note is the fact that there was almost a twofold lower concentration level of HCH in the waters of the atoll lagoon versus the ocean water surrounding the lagoon. The only obvious explanation was the presence of a temperature gradient, which entailed differing rates of photochemical and microbial transformation of the cyclohexane ring, and the accelerated evaporation that was taking place in the lagoon.

Another interesting finding was that the lagoon water of Caroline Atoll contained roughly one-half as much PCB as did the surrounding ocean water. Moreover, the composition of the CH's was significantly different: the lagoon water contained virtually no highly chlorinated PCB congeners, which was probably due to the higher rates of photochemical processes in the thoroughly heated shallow water of the lagoon. It should be noted, however, that as a general rule, PCB levels in the equatorial Pacific were only slightly lower than in the northern Pacific, even though sample composition turned out to be considerably different.

Whereas most of the PCB's in the Bering Sea consisted of di- and trichlorobiphenyls, the major constituents of PCB's in the equatorial waters were tri- and tetrachlorobiphenyls as well as heptachlorobiphenyls. Analysis of the CH's sorbed by suspended matter revealed a clear dependence of pollutant levels on latitude. For example, the content of HCH isomers in suspensions from the equatorial Pacific was almost 50 times lower than in the circumpolar parts of the ocean (Table 3). This may have been due to the significant shift in sorption-process equilibria associated with a 25°C rise in temperature. There was a marked (almost tenfold) change in PCB levels in suspended matter, whereas the levels in the water layer remained virtually constant. It is a curious fact that the equatorial Pacific is a unique region of the World Ocean where the PCB mixture appears to be equally apportioned between the suspended matter and the dissolved phase.

Of special interest is the distribution of the extensively used pesticide DDT in Pacific Ocean ecosystems. Dichlorodiphenyltrichloroethane levels in water samples from the Bering and Chukchi Seas have decreased considerably over the past decade due to restrictions on the use of this compound imposed by a number of industrialized countries. In fact, in some instances these levels come close to analytical zero (Chernyak *et al.*, 1989). In the equatorial Pacific, however, the DDT

TABLE 3

Chlorinated hydrocarbon levels ($\mu\text{g/g}$ dry weight) in suspended matter in the Pacific Ocean.

Station No.	Date	Depth (m)	Chlorinated Hydrocarbon			
			α -HCH	γ -HCH	DDT	PCB
113	09/21	0	54	43	135	258
Caroline Atoll	09/23-29	0	5	5	174	311
116	10/02	20	5	4	164	101
116	10/02	100	5	5	105	126
119	10/04	65	5	4	192	168
119	10/04	100	3	3	127	171
119	10/11	0	5	3	167	315
120	10/11	0	5	5	103	153
120	10/11	0	4	4	143	93
120	10/12	0	3	4	215	139
120	10/13	0	5	4	287	189
120	10/14	0	5	4	274	63
120	10/15	0	3	3	159	76
121	10/16	0	5	3	315	154
121	10/17	0	4	3	252	127
122	10/18	0	4	4	338	129
122	10/18	130	3	3	309	85
123		0	5	3	421	181
124		0	5	4	357	108

hazard remains considerable: its levels average 0.1 ng/l, which is typical of the areas most severely impacted by human activities, namely the North Atlantic and the Indian Ocean (Tanabe *et al.*, 1982).

Results for the microbial and photochemical degradation of PCB's in the equatorial Pacific are presented in Figs. 2–4. The gradual loss of several of the PCB congeners are plotted over time in Fig. 2. On incubation with natural populations of microbes from these central Pacific waters, some congeners were reduced by more than 50% in 10 days (e.g., BZ#s, Ballschmitter and Zell numbering system for PCB congeners; Ballschmitter & Zell, 1980) 7, 16, 49, 52, and 42. In Fig. 3, the degree of microbial degradation of the PCB's is organized by the PCB homologue group. From this presentation it is observed that the greater the degree of chlorine substitution of the biphenyl ring, the more resistant it is to microbial breakdown. Plotted for comparison are the relative rates of breakdown of the homologous groups for the two regions that were studied, the Bering Sea, and the central Pacific Ocean. Between these two locations, the rates of degradation of especially the mono- and dichlorobiphenyl homologues are faster in the warmer water of the Pacific. Figure 4 presents the times loss of total PCB's for the central Pacific based on a comparison between microbial degradation, photochemical degradation, and photochemical processes under the influence of added PAH's. It is apparent here that microbial degradation accounts for most of the breakdown in this area and that PAH's may have the capacity to inhibit photochemical breakdown of PCB's.

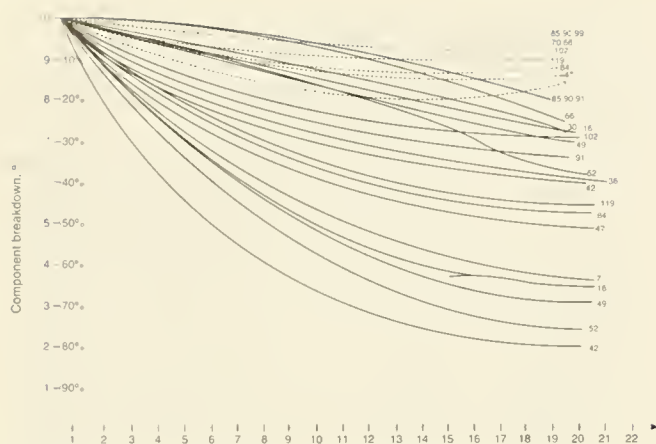


Fig.2. Photochemical breakdown of individual PCB components.

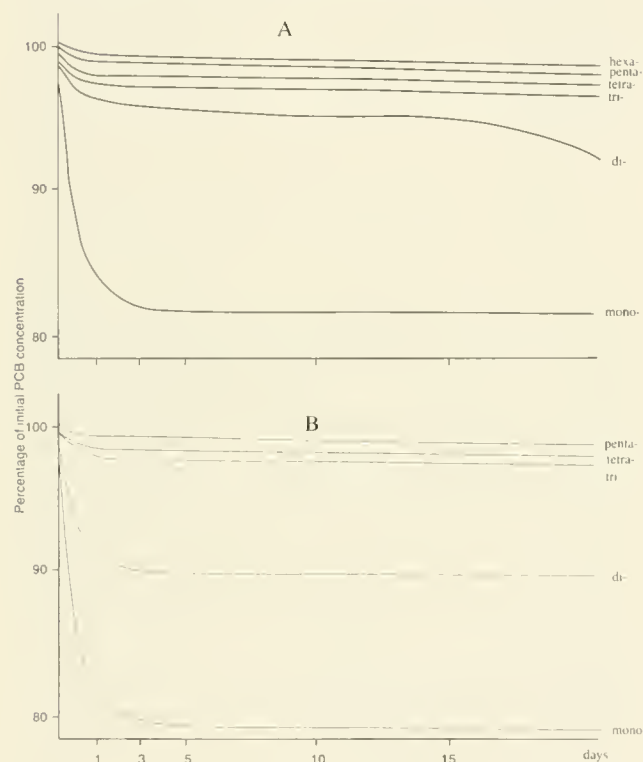


Fig.3. Microbial breakdown of PCB components in the waters of the Bering Sea (A) and central Pacific Ocean (B).

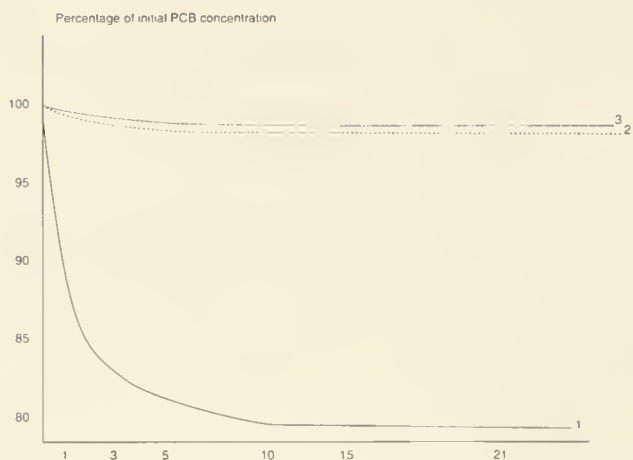


Fig.4. Breakdown of PCB's (dichlorobiphenyls) through microbial and photochemical action: 1) microbial; 2) photochemical; 3) photochemical in the presence of PAH's.

Conclusions

As a result of human activities, chlorinated hydrocarbons occur in all media constituting the Pacific ecosystems investigated. Levels of HCH isomers in the equatorial Pacific turned out to be lower than in polar areas. This is understandable, given the high volatility of this pollutant. Dichlorodiphenyltrichloroethane levels in certain parts of the Pacific (such as the Caroline Atoll) were found to be similar to those observed in impacted basins, although the concentration of this compound in the equatorial Pacific taken as a whole were not high. Polychlorinated biphenyls occurred in all the water samples studied. It is now clear that despite the slowness of photochemical and microbial breakdown of PCB's, these processes nevertheless play an important role in the self-purification of Pacific Ocean ecosystems.

2.2 Distribution of Polycyclic Aromatic Hydrocarbons

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Introduction

Three distinct regions (Caroline Atoll, tropical Pacific and South China Sea) during the First Joint US-USSR Central Pacific (BERPAC) Expedition were sampled and analyzed for polycyclic aromatic hydrocarbons (PAH's). Methods for collection and analyses are described in *Distribution of PAH's (Irha et al., 1992) in Results of the Third Joint US-USSR Bering & Chukchi Seas Expedition (BERPAC), Summer 1988* (Nagel, 1992). The regions that were sampled are identified in the Frontispiece to this volume.

Polychlorinated aromatic hydrocarbons are important natural and anthropogenic contaminants of marine ecosystems. These compounds are associated with petroleum pollution, including natural oil seepage, and with industrial contamination and many exhibit carcinogenic and mutagenic properties. In this paper, the presence and quantity of PAH's in both biotic and abiotic components of tropical Pacific ecosystems is reported.

Results

Caroline Atoll

Determinations were made of the composition and distribution of PAH's (Table 1) present in water and marine-organism suspensions sampled in inshore waters off the atoll, as well as in the following media: bottom sand, island soils, corals, and siphonales algae. The findings (Table 2) indicated that the PAH pollution of this ecosystem was negligible. There were no PAH's in samples of surface sand from the atoll, and the soils taken from a palm tree forest area showed PAH levels below background.

The total PAH content of coral samples did not exceed 9.6 µg/kg of dry weight. The following representatives of four- and five-ring PAH's were detected: benzo(e)pyrene (BeP), 62.5; indeno(1,2,3-cd)pyrene (IPy), 23; benzo(a)pyrene (BaP), 14.5 (in percent by weight).

The benthic sand of the atoll lagoons contained four- and five-ring PAH's (Table 2); the major constituents (in percent by weight of the total amount of PAH's present) were benzo(b)fluoranthene (BbF), from 38.7 to 53.6%; and BaP, from 16.8 to 36.6% (Fig. 1).

The surface waters off the atoll contained six four- and five-ring PAH's, whose total amount did not exceed 1.55 ng/l, the dominant constituents being the five-ring carcinogens BbF and BaP (Fig. 2). Suspended matter sampled

Table 1

List of specific PAH's identified by displacement-elutinal liquid chromatography

Name	Symbol	Structural formula	Carcinogenicity (Lee et al., 1981)
Pyrene	Py		0
Chrysene	Chr		+
Benzo(a)anthracene	BaA		+
Benzo(e)pyrene	BeP		0/+
Benzo(b)fluoranthene	BbF		++
Benzo(k)fluoranthene	BkF		++
Benzo(a)pyrene	BaP		++
Benzo(g,h,i)perylene	BPer		+
Dibenz(a,h)anthracene	DBA		+
Indeno(1,2,3-cd)pyrene	IPy		+

Note:

Classification	Symbol
noncarcinogenic	0
weakly carcinogenic	+
strongly carcinogenic	++

Critenon: % of animals that developed lesions.

0
33
>33

at a depth of 90 m included four kinds of four- and five-ring PAH's, whose total concentration was 0.68 ng/l, with the four-ring IPy and benz(a)anthracene (BaA) predominating (Fig. 2).

The total PAH level in the gills of Mexican (northern red, Pensacola) snapper (*Lutjanus campechanus*) specimens was moderate, amounting to 0.08 µg/kg; the corresponding value for muscle tissue was 1.13 µg/kg of fresh weight.

The following five-ring PAH's were identified as present in the gills (in percent by weight): BbF, 62.5; BaP, 33.5; benzo(k)fluoranthene (BkF), 3.7; moreover, chrysene (Chr) and benzophenanthrene (Bp) were also present. The main constituents of the total PAH mix were four-ring compounds: BaA, 88.5%, and Chr, 11.5%; also present were traces of BbF and BkF.

Polycyclic aromatic hydrocarbon levels in various components of the Caroline Atoll ecosystems indicated that this area was only slightly polluted by these specific compounds.

TABLE 2

PAH levels in particular media of the Caroline Atoll ecosystem (September 1988).

Medium	Units	Py	BaA Chr	BbF	BkF	BaP	Bep
Water, surface layer	ng/l	qualitatively present	tr.	1.25	0.90	0.21	tr.
Suspension (90 m)	ng/l	0.6	0.8	-	tr.	tr.	-
Benthic sand, lagoon	μ/kg	-	-	-	-	-	-
Lagoon I		-	-	-	-	-	-
Lagoon III		-	tr.	0.44	0.08	0.30	-
Lagoon V		-	0.60	0.60	0.09	0.26	-
Atoll soil	μ/kg	-	-	-	-	0.83	-
Aeropora corals	μ/kg	2.2	-	-	-	1.4	6.6
Siphonales algae (Caulerpaceae)	μ/kg	-	-	-	-	0.07	-

tr. - trace

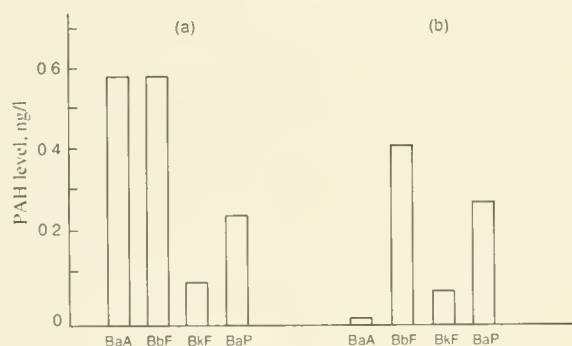


Fig. 1. PAH levels (μ/kg) in benthic sand of lagoons V (a) and III (b) of Caroline Atoll (September 1988).
[Legend:] A = PAH level, μ/kg.

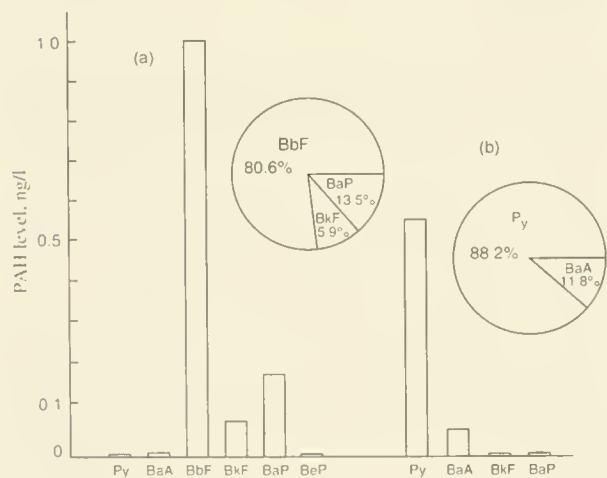


Fig. 2. Content of PAH's (ng/l) and their distribution (in percent by weight) in the surface (0-0.5 m) layer of water (a) and in a suspension (b) drawn from a depth of 90 m off Caroline Atoll (September 1988).
[Legend:] A = PAH level, ng/l.

Tropical Pacific

Polycyclic aromatic hydrocarbon levels in the surface waters were not high. In the open ocean, the total concentrations ranged from 0.8 to 43.8 ng/l, with a maximum of 396.6 ng/l in the Marianas sector. The composition and distribution of the PAH's identified in the surface waters of the open ocean indicated that the main compounds present were the following five-ring carcinogens (in percent by weight): BbF, 86.3; BkF, 11.0; BaA and Chr, 1.2; BeP, 1.0; BaP, 0.5; and IPy was present qualitatively.

The total PAH's present in the waters of the Marianas sector were 10 to 100 times higher in concentration than in the open ocean. The dominant compounds were four- and five-ring PAH's (in percent by weight), namely BaA and Chr, 38.7; BeP, 35.2; and pyrene (Py), 22.7. The BbF and BaP constituted 3.2% and 0.2% by weight, respectively.

In areas where PAH levels in the water were below the sensitivity threshold of the liquid chromatography technique employed, a more sensitive method for just BaP was employed. Benzo(a)pyrene is useful as a representative tracer of other PAH's (analytical methods described in Irha *et al.*, 1992). The following BaP levels were noted: up to 0.58 ng/l in the open ocean and up to 1.36 ng/l in the Marianas sector.

Unlike the surface layer of water, suspended matter sampled in the tropical Pacific was found to contain as many as 10 four- to six-ring PAH's. All samples taken at depths of 0, 20, 58, 80, 130, and 200 m contained the PAH's IPy, BaA, Chr, BbF, BkF, and BaP, the dominant ones being IPy and BaA, which accounted for 30-99% and 30-50%, respectively, of the total amount present. In certain instances, suspensions from various depths also contained IPy and benzo(g,h,i)perylene (BPer).

Bottom sediments of the tropical Pacific were found to contain only three kinds of four- and five-ring PAH's, namely BaA, BbF, and BaP, with the total PAH content not exceeding 4.5 μg/kg. The dominant PAH (by weight) was BbF, which accounted for 93% of the total amount of PAH's present. Although the composition of PAH's in the bottom sediments of the Marianas sector of the Pacific was similar, IPy and BbF were the dominant PAH's (50.7% and 47.3%, respectively, of the total weight of PAH's present).

South China Sea

Polycyclic aromatic hydrocarbon levels in the waters of the South China Sea were much higher than in the open ocean and in the Marianas sector (Table 3). The total amount of PAH's in the water varied widely: the PAH mixture identified in the surface microlayer consisted largely of four- and five-ring PAH's (in percent by weight): BeP, 45.5; BaA and Chr, 28.7; Py, 24.6; BbF, 0.9; and BaP, 0.2. Their weight ratios and composition in the surface layer were somewhat different (Table 3), moving towards increased fractions of BaA and Chr, and BeP. Considerably higher levels of PAH's, by weight, were detected in the benthic portion of the water column, the dominant PAH being BbF (Table 3).

In those sea areas where the PAH level fell below the analytical detection limit, the BaP level did not exceed 1.58 ng/l.

TABLE 3

PAH levels in particular media of the South China Sea ecosystems (Station 127, September 1988).

Medium	Units	Py	BaA	BeP	BbF	BkF	BaP	IPy	BPer	DBA
Water, surface	ng/l	qualitatively	tr.	170	67	-	4.5	-	-	-
microlayer		present								
Water, surface layer (0 to 0.5 m)	ng/l	150	175	278	5.5	-	1.6	-	-	-
Benthic layer	ng/l	qualitatively present	290	290	14,000	-	300	-	-	-
Benthic sediment	μ/kg	-	-	-	0.46	0.14	0.15	-	-	-
Neuston	μ/kg	-	1.4	1.6	1.7	-	1.3	0.6	0.6	-
Suspension, 58 m	ng/l	4.7	0.6	0.9	0.06	0.01	0.07	tr.	0.07	tr.
Suspension, 80 m	ng/l	1.8	0.6	1	0.4	0.01	0.04	tr.	0.06	tr.
Hydroids	μ/kg	-	-	-	6.5	0.6	0.7	-	-	-
tr. - trace										

The total PAH level in the suspended matter drawn from depths of 58 and 80 m were 6.4 and 3.9 ng/l, respectively (Table 3). The PAH mix was found to contain ten four- to six-ring PAH's in the following relative amounts (in percent by weight): IPy, 65.2; BeP, 17.4; BaA and Chr, 11.0; BeP, 1.0; BPer, 1.0; BbF, 0.9; BkF, 0.2; and IPy and dibenz(a,h)anthracene (DBA) were present in trace amounts.

The sediment samples contained three five-ring carcinogenic PAH's (Table 3), namely BbF, BkF, and BaP. The total PAH content of the sediment did not exceed 0.75 μg/kg of dry weight, the dominant constituent being BbF (61.3% of the total content by weight).

The PAH mix detected in the marine biota indicated that PAH's were fairly abundant. The total PAH content of the neuston of the South China Sea was 6.6 μg/kg (Table 3). The mix consisted of six PAH's. Most of the total amount was made up of four- and five-ring compounds (i.e., BaA, BeP, BbF, and BaP).

It should be noted that the PAH mix detected in the marine hydroids was similar to that found in the sediment (Table 3) and consisted of strongly carcinogenic five-ring compounds, namely BbF, BaP, and BkF. Their total content in the hydroids was 10 times that in the sediment, and the weight ratios reflected a

larger fraction of BbF, 83.3%. The relative content of BaP and BkF was 8.9% and 7.6%, respectively. The same carcinogenic PAH's were detected in benthic organisms (*Petrosia* sponges, Table 4).

TABLE 4

Comparative PAH levels in sponge tissues (μ/kg of dry weight) and fish livers (μ/kg of fresh weight) from the South China Sea (1) and Bering Sea (2).

PAH	1		2	
	Sponge	Shark liver* n = 2	Sponge	Liver of walleye pollack
Chr	-	6.15	-	34.00
BbF	0.70	0.27	0.90	4.50
BkF	0.09	0.22	0.16	tr.
BaP	0.40	1.00	0.60	13.00
BaA	qualitatively present	1.00	-	qualitatively present
BPer	-	2.80	-	-

* Specimens caught in the tropical Pacific.

It may be noted that the total content and mix of PAH's present in the tissues of South China Sea sponges was not much different from those established for the same aquatic organisms in the Bering Sea (Table 4). The predominant PAH's (in percent by weight) for South China Sea and Bering Sea sponges were BbF (54 and 59) and BaP (36 and 33.6), respectively.

Concentrations of PAH's in livers of sharks ranged from 1.2 to 10.2 µg/kg of fresh weight (Table 4). The predominant compounds were the following four- and five-ring PAH's

(in percent by weight): Chr, 53.7; BPer, 24.7; BaA, 8.7; BaP, 8.7; BbF, 2.3; and BkF, 1.9.

For comparison we note that the levels and distribution of PAH's in aquatic organisms of the Bering Sea (sponges and walleye-pollack liver) also indicate relatively high total PAH's in fish livers and the buildup of the strong carcinogens BbF, BaP, and BkF as the dominant PAH's in sponges (Table 4).

Analysis of the findings of the present study points to severe petroleum hydrocarbon pollution of the sea and to the buildup of the carcinogenic PAH's—BbF and BaP—in some aquatic organisms.

2.3 The Occurrence and Microbial Transformation of Benzo(a)pyrene in the Waters of the Tropical Pacific (Caroline Atoll, Line Islands, Phoenix Islands Transect, South China Sea)

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Introduction

Among the numerous organic pollutants working to produce dangerous and undesirable changes in the chemical and biological status of the marine environment, polycyclic aromatic hydrocarbons (PAH's) of both natural and human origin must be singled out as being particularly noxious. Exhibiting considerable molecular stability, as well as pronounced carcinogenic and mutagenic properties, compounds of this series are a serious hazard to marine life. At present, researchers have been choosing benzo(a)pyrene (BaP) as an indicator of environmental pollution by PAH's.

Benzo(a)pyrene and other PAH's have been found to occur in many marine ecosystem components from the arctic latitudes (Volodkovich & Belyaeva, 1987) all the way to the Antarctic, affecting mariculture and other activities.

The proximity of human sources of pollution has a powerful impact on the marine environment, increasing BaP levels in waters by factors ranging from tens to hundreds (Tsyban *et al.*, 1985b; Tsyban *et al.*, 1986).

For example, BaP levels in some parts of Los Angeles harbor have reached, and even exceeded, 118 ng/l, while concentrations in the top 0.5 m of the water column in the equatorial Pacific have been reported in the 1–6 ng/l range (Shilina, 1982).

In view of the fact that elevated PAH levels in seawater are due largely to the proximity of a given sea area to pollution sources, the study of BaP circulation and elimination processes (including microbial transformation) in as yet unimpacted open sea and open ocean areas is of considerable interest and value.

Microorganisms, which are virtually ubiquitous in the World Ocean, play a major role in the functioning of marine ecosystems and in the biochemical cycling of various compounds, including pollutants such as petroleum crude and PAH's (Izrael & Tsyban, 1989). The processes involved in the microbial transformation of aromatic hydrocarbons and heterocyclic compounds have been investigated in sufficient detail. On the other hand, the rates of microbial degradation of BaP in the marine environment, as well as the local and regional scale of these processes, have thus far been neglected (Tsyban *et al.*, 1986).

Integrated studies of biogeochemical cycling of PAH's, using BaP as an example, were performed in 1988 during the cruise of the R/V *Akademik Korolev* as an extension of work begun in 1981 in the South China Sea and the Marianas sector. The research represented the first time that such work has been undertaken in the tropical Pacific (in the Caroline Atoll area and the Line Islands/Phoenix Islands transect).

Methods

Sampling

The studies were performed on both rainwater and seawater samples taken from a variety of depths ranging from the surface down to the benthic portion of the water column. Also investigated were natural bacterioplankton communities in surface and near-surface layers.

Seawater samples were taken with Niskin bottles. Rainwater samples were collected in vessels of surface area 0.5 m² mounted near the bow of the vessel. The BaP present in the water was extracted from 1-l samples by triple benzene extraction. Final processing and analysis of 100 ml volumes of benzene extract of BaP were carried out ashore upon completion of the cruise.

Seawater samples for use in the microbiological experiments were taken using sterile sampling equipment (a 5-l plastic Niskin bottle, and a 5-l glass bottle, in the case of Caroline Atoll lagoon). The water samples containing natural microorganism communities were decanted into glass bottles under sterile conditions. Further processing was carried out in the shipboard microbiology lab.

The In Situ Experiments to Assess the Biodegradation Potential of Seawater Microflora in Relation to BaP

The process involved in the microbial transformation of BaP was studied under the conditions similar to the *in situ* experiments. These involved placing 250-ml samples containing natural microflora communities in dark glass bottles of volume 0.5 l. A weighed amount of BaP dissolved in a minimum quantity of acetone (0.05 ml) was added to the bottles immediately after addition of the water (the acetone evaporated within a few minutes). The transformation process was simulated in runs using BaP concentrations of 2 and 10 µg/l. In order to allow for abiotic factors, each experiment included a control in the form of a sample of sterile water drawn from the same depth and containing the same concentration of BaP. Each complete pair of tests (experiment plus control) was run three times.

In order to make the conditions of the *in situ* experiments as close as possible to natural, the series of glass vessels were placed in baths with running water from the surrounding sea, with the baths themselves mounted on the deck of the research vessel. In the case of the Caroline Atoll, the sample-containing vessels were placed in a plastic cassette placed on the bottom of the lagoon (at a depth of 8 m). Exposure equaled 5–7 days, depending on the seawater temperature. On completion of exposure, the microbial activities were terminated by adding several milliliters of concentrated hydrochloric acid to the sample. The residual BaP in the experimental and control samples were extracted using benzene. The final BaP concentration values were determined ashore.

Chemical Analysis

Quantitative determinations of the residual BaP levels in the seawater samples involved concentrating the resulting benzene extracts down to a volume of 1 ml and then analyzing them on alumina plates using thin layer chromatography with heptane–benzene–acetone (100:60:6.7, by volume) as the solvent system. The BaP-containing area of the adsorbent was eluted with acetone, after which the BaP was transferred to *n*-octane.

The benzene extracts of BaP that were obtained in the microbial experiments were treated without chromatographic thin-layer separation. The evaporated portion of the benzene extracts were eluted with 2-ml solutions of *n*-octane containing 1×10^{-7} g/ml of 1,12-benzopyrene, which was used as an internal standard.

Quantitative determinations of BaP (in *n*-octane solution) were made by a fluorescence-spectrum analysis method, relying on the Shpolsky effect (Shpolsky *et al.*, 1952; Fedoseeva & Khesina, 1968). The analyses were performed with a DFS-12 spectrograph at a temperature of -196°C using supplementary standards (BaP and other compounds). The minimum sensitivity of the method for BaP was 1×10^{-10} g/ml, with error brackets of 10%.

The simulated rates for microbiological degradation were determined from the difference between the initial (introduced) and the final (remaining) mass of BaP in the separate reactors.

Results and Discussion

The first series of studies concerned the equatorial Pacific (Fig. 1) in the rectangle bounded by 7° and 0°S and 150° and 180°W. Analysis of the findings showed that BaP levels in the waters of the Line Islands/Phoenix Islands transect were remarkable for their extreme purity. Benzo(a)pyrene levels in the waters of the transect down to depths of 2,000 m corresponded to the minimal background value of 1 ng/l and lower. Certain samples contained no detectable amount of BaP whatever (Table 1). Thus, the average BaP level for the entire water column at Station 117 was just 0.06, 0.018 ng/l. In the majority of cases, the BaP levels did not exceed 5 ng/l. As seen in Fig. 2, zones with elevated BaP levels were of a local character. High levels were recorded for depths of 1,000–1,500 m (6.5 and 11.3 ng/l, respectively), with only one instance (10.3 ng/l, Station 118) of a high concentration in the top 0.5 m of the water column. It must be emphasized that the peak levels recorded were a whole order of magnitude lower than BaP levels in open ocean and other portions of the Pacific as found in earlier studies (Izrael & Tsyban, 1989). The limited occurrence and low levels of BaP buildup in seawater along the Line/Phoenix transect may be attributed not only to the remoteness of this geographic region from the principal human sources of pollution (industrialized areas and shipping routes) but also to the absence of any pronounced PAH flows in this ultraoligotrophic part of the ocean. Nor does economic activity in the waters of the Kiribati Republic archipelago appear to be having any significant deleterious effect on this marine environment.

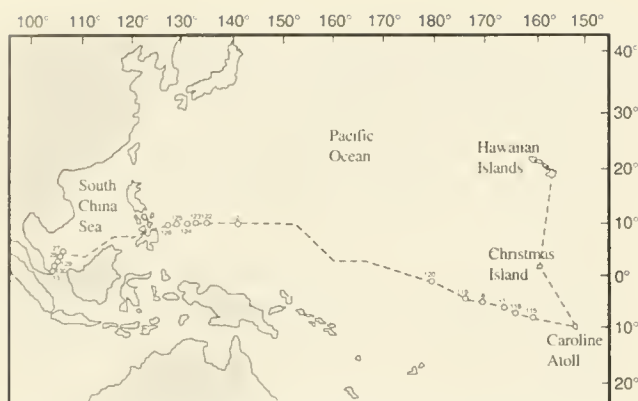


Fig.1. Expedition route and station locations in the Pacific Ocean and South China Sea (9 September to 31 October 1988).

If this minimal concentration of BaP serves as an indicator representing a whole series of carcinogenic PAH's, then the equatorial zone in question can be readily classified as one of the "background" portions of the World Ocean.

The studies at Caroline Atoll (10°N, 150°W) indicated that BaP was present in individual water samples both from the interior portion of the lagoon and from the inshore waters at

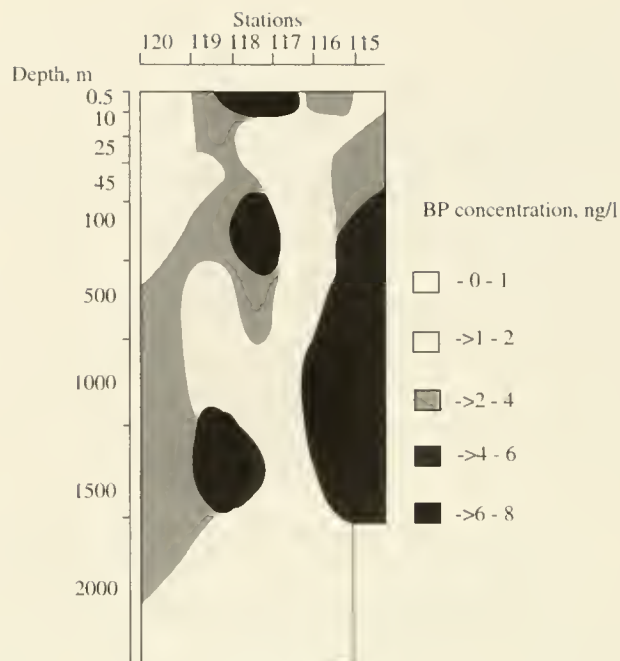


Fig.2. Occurrence of benzo(a)pyrene in the waters of the Line/Phoenix transect between 7°S and 0°S in the equatorial Pacific (October 1988).

TABLE 1

Benzo(a)pyrene concentrations (ng/l) in the waters of the central Pacific (September and October 1988).

Region	Station No.	Depth, m								
		0.5	10	25	45	100	500	1,000	1,500	2,000
Caroline Atoll	--									
Lagoon		0.0	0.1			0.1	0.1			
Inshore waters	114	0.2	0.1	0.1	0.0	0.1				
Line/Phoenix transect	115	0.4	1.0	3.7	2.5	4.7	4.1	4.4	4.7	--
	116	2.5	1.4	0.6	1.3	1.5	4.1	6.5	0.9	0.9
	117	0.1	0.3	0.3	0.7	0.2	0.6	1.1	1.2	0.9
	118	10.3	0.0	1.1	2.1	5.8	0.6	1.6	5.9	--
	119	2.4	3.7	2.2	1.4	7.2	1.9	11.3	6.5	0.5
	120	2.0	0.6	0.0	0.3	1.0	2.9	2.7	2.8	0.6
Marianas transect	121	80.0	7.0	5.9	9.2	3.6	5.5	5.3	2.5	2.7
	122	104.0	96.0	94.0	101.0	86.0	6.6	9.7	111.0	96.0
	123	57.5	84.0	94.0	62.0	84.0	56.0	39.3	6.7	5.0
	124	38.2	96.6	68.4	5.0	14.0	12.5	6.6	14.5	0.8
	125	2.7	1.1	3.5	11.3	1.6	2.3	2.1	0.9	10.8
	126	12.2	12.1	2.3	1.9	3.0	9.0	14.3	1.0	6.2
South China Sea	127	2.0	3.2	0.9	16.0	173.0*				
	127	1.1	2.3	0.9	0.6	105.4*				
	129	18.5	8.2	3.2	12.4	9.3	27.5**			
	131	64.8	17.1	11.0	6.0	10.0	148.8***			

Sea-bottom depths:

* - 61 m

** - 200 m

*** - 250 m

depths of up to 100 m. However, these also corresponded to background values not exceeding 0.2 ng/l and averaging 0.08 ng/l (Table 1). Particularly noteworthy was the absence of BaP in the top 0.5 m of the water column inside the lagoon.

Without excluding the possibility of PAH biosynthesis in the highly productive coral ecosystem of Caroline Atoll (such as the phenomenon reported for the Clipperton Lagoons; Niassat *et al.*, 1968), it may be assumed, with some confidence, that the high rates of photochemical oxidation and microbial transformation of PAH's characteristic of equatorial waters are conducive to the elimination of PAH's from the waters of Caroline Atoll and especially from the surface layer.

Quite the opposite situation was observed in the Marianas trough region along the Marianas transect (between 142°E and 128°E, along 11°N) (Fig. 3). Whereas the BaP levels at the extremities of this sector, with one exception, ranged from 0.9 to 9.2 ng/l (Table 1), the water column in the central portion of the transect (Stations 122 and 123) contained elevated and even maximum concentrations (up to and over 100 ng/l). As is evident from Fig. 3, high BaP levels from 38 to 104 ng/l were noted not only in the surface layer but also in deeper waters. Thus, the BaP concentration in the upper 100-m water layer at Station 122 averaged 96.2 ng/l, while the average value at 1,500–2,000 m was 103.5 ng/l. The lowest BaP concentrations occurred at the western end of the transect, where the BaP

levels at Stations 126 and 125 in waters up to 2,000 m deep were 4.03 and 6.88 ng/l, respectively. The average value for eastern Station 121, at depths from 10 to 2,000 m, was 5.17 ng/l.

Analysis of rainwater samples taken at 11°N along the transect had BaP levels of 7.2, 8.8, and 9.2 ng/l; that was one order of magnitude lower than the levels in rainwater measured along the transect in 1981 (Izrael & Tsyban, 1989). Nevertheless, these findings point to the possible contribution of PAH's to the Marianas sector of the Pacific via long-distance atmospheric transport of organic pollutants.

High BaP levels (up to over 100 ng/l) were noted in the waters of the Marianas sector during the previous study period in 1981 (Izrael & Tsyban, 1989). These ranged from 80 to 120 ng/l. However, the pollution in all instances was confined to the top 2 m of the water column with peaks in the surface microlayer (SML).

Since most of the waters of the Marianas sector lie in the area of influence of the northern branch of the tradewind current, it may be supposed that the invasion of deeper layers by pollutants (including BaP) occurs through downwelling of surface water due to the anticyclonic circulation of water masses in this region.

The BaP levels in the southwestern South China Sea had a broad range of values from 0.9 to 173 ng/l (Table 1). The lowest BaP levels occurred in open waters at Station 127 (Fig. 1). Two days of work at this station yielded similar estimates, the BaP levels over most of the water column varying from 0.6 to 2.0 ng/l and averaging 1.5 ng/l. The bottom layer (at a depth of 61 m) exhibited a very high BaP concentration and with an average value of 139.2 ng/l, indicating severe PAH pollution.

The BaP concentrations in the waters of stations lying close to the eastern coast of Singapore (Stations 129 and 131) had elevated BaP concentrations in the 10 to 100-m layer of the water column (averaging 8.2 and 13.2 ng/l, respectively). The maximum BaP levels were detected in the top 0.5 m layer on the one hand and at the sea bottom on the other. These were as high as 148.8 ng/l (Table 1).

This peculiar pattern of BaP level distribution over the water column can be attributed to the influx of PAH's with the oil pollution that impacts the surface waters at the stations in question as well as the deeper waters below. It should be noted that the areas of the South China Sea investigated are busy maritime thoroughfares for vessels carrying both crude oil and refinery products as well as sites of intense offshore drilling activity.

The potential physiological ability of microflora to transform BaP in the central Pacific was studied in a series of *in situ* experiments using natural bacterioplankton communities from Caroline Atoll and the southwestern portion of the South China Sea.

The results of the process simulations expressed in terms of the degree of elimination of the artificially-introduced amount of BaP are shown in Fig. 4. The bacterioplankton of the marine areas investigated were able to transform the polyaromatic hydrocarbon in question. On the whole, the level of microbial degradation reached 57–98% of the mass of BaP introduced into the samples (Table 2). In order to gain deeper

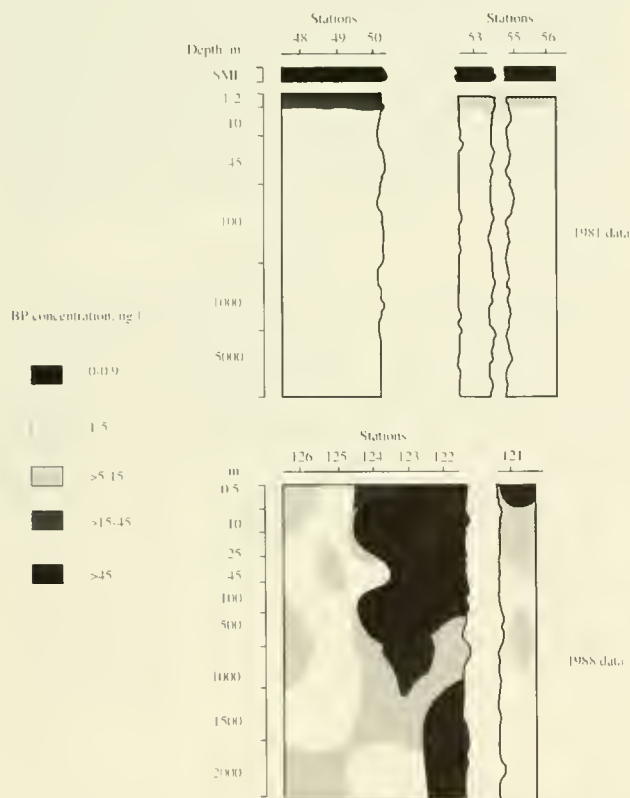


Fig.3. Distribution of benzo(a)pyrene in the waters of the Marianas transect along 11°N (between 142°E and 138°E) in the tropical Pacific in 1981 and 1988.

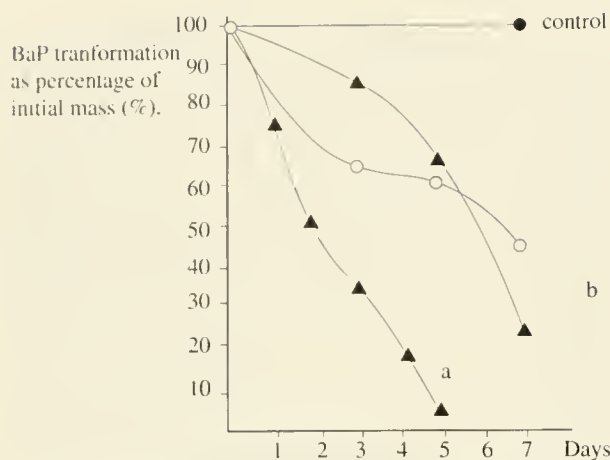


Fig.4. Dynamics of BaP transformation in the *in situ* experiments using microflora from waters of Caroline Atoll lagoon (a) and from the South China Sea (b) at Station 127 (1988 data). (Initial BaP concentration: ▲- 2 µg/l; ○- 10 µg/l; ●- control)

insight into the natural processes of BaP elimination from the marine environment, we also undertook a study of the dynamics involved in microbial transformation. The results obtained from individual runs of each experiment yielded reasonably consistent values.

As may be seen from Fig. 4, the highest microbial transformation rates were noted in experiments using microflora taken from Caroline Atoll lagoon water. The series of samples placed in natural conditions at a depth of 8 m contained just 50% of the initially introduced amount of BaP (initial concentration 10 µg/l) after only 2 days; after 5 days had elapsed, 97% of the initial BaP had been transformed. The rate of microbial transformation of BaP in the lagoon waters was high, with the curve of the degradation process close to linear.

The rate of microbial transformation of BaP in the South China Sea was much lower than for the atoll. With an initial BaP concentration of 2 ng/l, only one-third of its initial mass had been transformed after 5 days. However, after 7 days of the experiment, the microflora from the top 0.5 m of the water column was able to transform as much as 77% of the introduced BaP. With a higher concentration (10 µg/l), microbial transformation in the experiment produced a consistent value, 34% of the initial mass over the third through the fifth days of the experiment where a period of decreased microfloral activity occurred (Fig. 4), the incremental transformation amounting to just 0.6 µg of BaP. In these tests, the total mass of the BaP degraded after 7 days; at the time which the experiment was terminated, the mass did not exceed 5.68 µg (56% of the initial concentration). On the whole, the rate of microbial transformation of BaP turned out to be not particularly dependent on the initial concentration (2 and 10 µg/l). Assuming the process curve to be more or less linear for both the equatorial and the tropical Pacific, we were able to estimate the average rates of microbial transformation of BaP. The resulting values were 1.94 µg/l/day for the waters of Caroline Atoll and 0.81 µg/l/day for the South China Sea.

The abilities of marine microflora to degrade BaP are therefore relatively high. In the case of the Caroline Atoll, the biodegradation rates exceeded those of similar processes investigated in impacted areas such as the Baltic Sea (Tsyban *et al.*, 1985a). The results of our 1988 studies demonstrate the need to consider PAH, and especially BaP, metabolism as an exceedingly important process for detoxification through the elimination of the pollutants in question from the highly dynamic ecosystem that constitutes the tropical zones of the World Ocean.

TABLE 2

Dynamics of benzo(a)pyrene transformation by microflora from central Pacific waters in the *in situ* experiments (October 1988).

Region of Operations and sampling depth, m	Exposure, days	BaP concentration, µg/l		Microbial transformation of BaP, in % of concentration C _i
		Initial C _i	At end of experiment Control Exp.	
Caroline Atoll Lagoon, 8 m	0	10	9.9	0
	1	10		7.8
	2	10		4.9
	3	10		3.5
	4	10		1.8
	5	10		0.3
	5	10	9.9	0
South China Sea, Station 127, 0.5 m	0	2.0	2.0	0
	3	2		1.71
	5	2		1.37
	7	2		0.46
	7	2	2.0	0
Same as above	0	10	10	0
	3	10		6.62
	5	10		6.00
	7	10		4.32
	7	10	9.9	0

2.4 Cesium-137 in the Surface Waters of the Central Equatorial Pacific

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Introduction

The study of radioactive contamination of ocean waters throughout the world is one of the most important tasks facing researchers concerned with the effects of human activities on the ocean environment. Man-induced radioactivity of the marine environment has three origins: 1. nuclear weapons testing; 2. nuclear power plant operation; and 3. operation of nuclear fuel treatment and reprocessing plants.

The need for more information about the present status of radioactive contaminants of World Ocean waters prompted our research efforts in the course of the 47th cruise of the R/V *Akademik Korolev* in the central portion of the central equatorial and western Pacific from September to November 1988.

The indicator of radioactive pollution selected was cesium-137, a radionuclide with a long half-life. It is this radionuclide, together with strontium-90 and plutonium-239, that presents the greatest potential threat to the marine environment.

Methods

Seawater samples of large volume (0.8–1.1 m³) were drawn from various depths (0–200 m) using NIVA and Malysk immersion pumps. Selective extraction of the cesium-137 was performed with the aid of Milton-T fibrous sorbent impregnated with copper ferrocyanide (Vakulovsky, 1986). Following extraction, the sorbent was reduced to ash in a flameless muffle furnace at a temperature not exceeding 450°C. The ash residue was then hermetically sealed in a polyethylene capsule. In December 1988, the samples were measured using a gamma-spectrometry setup at one of the laboratories of the State Oceanographic Institute, Odessa Branch. The error of the cesium-137 determinations did not exceed 10%. The detection threshold was 0.01 Bq.

Results

Cesium-137 levels in surface waters were determined in the central equatorial portion of the Pacific, as well as in the Philippine, South China, East China, and Japan Seas. The results are summarized in Table 1. Figure 1 shows the location of cesium-137 level measurements in the surface (0–3 m) layer of Pacific Basin waters along the expedition route.

Analysis of the data showed that the spatial distribution of cesium-137 levels was very uneven. The absolute minimum and maximum concentrations were recorded in the equatorial Pacific. The minimum level recorded in the course of the entire expedition was situated at 8°N, 156°35'W between Hawaii and Christmas Island. This was at a time when the *Akademik Korolev* was traversing the northern boundary of the intratropical convergence zone. Precipitation was abundant, and the resulting dilution was what, in our view, lowered the cesium-137 concentration in the top layer down to 0.7 Bq/m³.

A maximum concentration of 7.0 Bq/m³ was recorded in the vicinity of Kusaie Island in the Carolines group.

During this period, the vessel was at its shortest distance from the Marshall Islands that include the Bikini and Eniwetok Atolls, sites where nuclear weapons were tested in the 1950's. The elevated levels observed were attributable either to the transport of the cesium-137 enriched water masses from the Marshall Islands or to the presence of the local sources on the Kusaie Island, lying eight miles north of the cruise track. A more detailed survey of the region might allow identification of sources.

Elevated (3.4–3.9 Bq/m³) cesium-137 levels in the waters off Tarawa and Caroline Atolls and Christmas Island may have been due to the transport of oceanic waters from the Tuamotu Archipelago, where nuclear weapon testing is regularly conducted by France. The considerable difference between the cesium-137 levels in samples taken two miles off Caroline Atoll and those measured in the waters of its lagoon was especially noteworthy.

The cesium-137 level in the lagoon water was double the value obtained for oceanic water taken off the atoll. This may be attributed to cesium-137 enrichment of the inner lagoon waters by the flushing of radionuclides deposited on the atoll surface by atmospheric fallout. Analysis of the average levels of cesium-137 for each region (Table 2) showed that the 'cleanest' waters of all the ocean areas studied were those of the equatorial Pacific. In terms of radioactive pollution, this region must be ranked between the Bering Sea (Medinets *et al.*, 1992) and the rest of the regions of the Pacific.

The findings of the present study agree with the results obtained by Japanese researchers who worked in the central Pacific in 1980–82 (Nagaya & Nakamura, 1985).

TABLE 1

Cesium-137 levels in Pacific Ocean waters in the autumn of 1988.

Date	Coordinates		Sampling depth (m)	Mean levels Bq/m ³
	Latitude	Longitude		
09-15	8°00' N	156°35' W	0 - 3	0.7
09-16	4°40' N	157°04' W	0 - 3	2.7
09-18	1°28' N	157°43' W	0 - 3	2.6
09-19	1°16' N	156°00' W	0 - 3	3.5
09-20	5°49' S	153°05' W	0 - 60	3.6
09-21	6°53' S	153°21' W	0 - 70	2.9
09-25	9°59' S	150°15' W	0 - 100	1.9
09-28*	9°59' S	150°15' W	0 - 3	3.9
10-02	6°37' S	161°44' W	0 - 100	3.6
10-04	3°48' S	172°03' W	0 - 100	2.2
10-07	0°16' S	177°38' E	0 - 20	2.0
10-08	1°20' N	172°20' E	0 - 100	1.9
10-11	2°41' N	168°17' E	0 - 3	3.3
10-11	3°03' N	161°01' E	0 - 3	2.3
10-12	4°20' N	162°27' E	0 - 3	7.0
10-13	7°21' N	156°42' E	0 - 3	4.4
10-14	10°08' N	153°45' E	0 - 3	5.9
10-15	10°16' N	147°45' E	0 - 3	3.4
10-16	11°12' N	142°55' E	0 - 3	2.9
10-17	11°15' N	139°35' E	0 - 3	3.0
10-18	11°00' N	136°00' E	0 - 120	4.4
10-18	11°05' N	134°07' E	0 - 3	4.9
10-19	11°00' N	132°21' E	0 - 3	3.7
10-20	11°00' N	130°33' E	0 - 3	3.3
10-21	10°59' N	128°46' E	0 - 200	5.5
10-24	5°12' N	114°05' E	0 - 3	6.2
10-25	5°30' N	109°27' E	0 - 3	5.3
10-27	6°00' N	106°54' E	0 - 50	5.2
10-27	6°00' N	106°54' E	0 - 50	5.2
10-28	5°14' N	106°27' E	0 - 55	4.2
10-28	5°14' N	106°27' E	0 - 60	4.5
10-29	4°18' N	105°54' E	0 - 80	4.8
10-29	3°23' N	105°19' E	0 - 60	4.3
10-30	2°19' N	104°54' E	0 - 40	3.4
11-06	4°20' N	106°42' E	0 - 70	5.9
11-07	4°41' N	11°47' E	0 - 70	5.2
11-08	8°04' N	116°13' E	0 - 3	4.9
11-09	11°35' N	118°42' E	0 - 3	6.3
11-10	17°26' N	119°53' E	0 - 120	4.9
11-11	21°16' N	121°43' E	0 - 10	4.8
11-12	24°58' N	123°39' E	0 - 10	4.3
11-13	29°00' N	127°00' E	0 - 10	4.3
11-13	32°47' N	128°09' E	0 - 10	4.4
11-14	36°41' N	130°52' E	0 - 10	5.3
11-15	41°11' N	132°12' E	0 - 10	4.7
11-15	43°01' N	131°59' E	0 - 10	5.6

* Sample drawn from the lagoon of Caroline Atoll.

TABLE 2

Mean cesium-137 levels in seawater by region.

Region	Mean level Bq/m ³
Bering Sea (50-60° N) (from Medinets <i>et al.</i> , 1992)	2.4 ± 0.2
Pacific Ocean (10-40° N) (from Nagaya & Nakamura, 1985)	5.2 ± 0.3
Equatorial Pacific (5°N-10°S)	3.6 ± 0.3
South China Sea	5.0 ± 0.2
East China Sea	4.3 ± 0.1
Sea of Japan	5.2 ± 0.3

Fig. 1. Map of sampling locations to determine cesium-137 levels (Bq/m³) in the surface layer (0-3 m). (●) denotes results obtained in the present study; (◇) denotes results reported by Nagaya & Nakamura, 1985)

Comparison of the overall radiation picture in the Pacific region with our findings on the contamination status of the Black and Baltic Seas conducted from 1986 to 1988 shows that cesium-137 concentrations in the Pacific are, at present, 10 to 20 times lower than in the seas of the European region impacted by local resources.

2.5 Quantity and Distribution of Plastics: An Analysis of Chemical Hazards to Marine Life

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Introduction

In recent years, plastics in the marine environment have been recognized as important pollutants of marine ecosystems (Laist, 1987; Pruter, 1987; Wolfe, 1987). Medical waste, plastic debris, and other types of refuse have washed ashore on Atlantic Coast beaches at alarming rates. These events have created new public awareness of the critical nature of the plastic waste disposal. Plastics present a unique disposal problem because the same attributes that make many types of plastics useful also enhance their longevity and buoyancy in the world's oceans.

The distribution of plastics has been studied in various estuarine, coastal, and oceanic waters of the world. Concentrations of plastics in surface waters have been associated with oceanic convergence zones or the proximity to shipping lanes (Colton *et al.*, 1974; Wong *et al.*, 1974; Wolfe, 1987). Although the distribution and abundance of plastics in the oceans have been studied almost exclusively in surface water, it is well known that many types of plastics do not float and must occur in marine sediments (Shaw, 1977). Gradual sinking of those plastics that do float is also possible as bacteria, diatoms, hydroids, and other marine life grow on the surface of floating plastics (Carpenter *et al.*, 1972; Colton *et al.*, 1974; Winston, 1982). Morris (1980) indicated that floating plastics gradually sink to the bottom or to a denser horizon where they attain neutral buoyancy and remain in suspension. Because the stratum of the pycnocline represents a marked change in water density, this would appear to be a likely area for subsurface accumulation of plastics with the appropriate neutral buoyancy.

Potential adverse effects of plastics in the marine environment include aesthetic, physical, and chemical. Clearly, floating plastic debris or litter that occurs on beaches is visually unpleasant. Physical impacts of plastics have been well documented. Entanglement and ingestion of floating plastics by sea turtles have been found in several areas (Balazs, 1985; Carr, 1987). Fish have been found to ingest plastic pellets (Carpenter *et al.*, 1972), as have seabirds (Connors & Smith, 1982; Furness, 1985; Day & Shaw, 1987; Fry *et al.*, 1987). In several studies seabirds were found to have consumed massive quantities of plastics (Day *et al.*, 1985; Furness, 1985; Fry *et al.*, 1987; Ryan, 1987). The physical ingestion of plastics has been detrimental with respect to causing digestive system impaction, ulcerative lesions, and reducing meal size

(Day *et al.*, 1985; Fry *et al.*, 1987; Ryan, 1988a). However, there continues to be much speculation regarding the potential chemical hazards of plastics to seabirds and other marine organisms.

Raw plastic pellets have generally been considered to be biologically inactive, although manufactured plastics often contain additives known to be toxic (van Franeker, 1985). Moreover, since Carpenter *et al.* (1972) published the first account of polychlorinated biphenyls (PCB's) adsorbing to plastic spherules in seawater, there has been concern for the potential for PCB exposure to fish and wildlife that ingest plastics. Ryan *et al.* (1988b) found evidence to suggest that seabirds assimilated PCB's from ingested plastic particles. However, Fry *et al.* (1987) suggested that plastics were unlikely to pose a significant toxic hazard to birds compared to the physical impaction effects that may result. Polychlorinated biphenyls are commonly found in certain types of plastics and the potential for plastics to adsorb PCB's from ambient water would suggest two possible sources of PCB contamination from marine plastics. One potential source would be intrinsic: PCB's incorporated into the plastic during manufacturing. A second source, extrinsic, represents PCB's adsorbed or absorbed from contaminated water. To date, there is still little known about the association of environmental contaminants occurring both in and on plastics in the marine environment and their potential toxic hazard to marine organisms.

In this paper we report the abundance and distribution of plastics in areas of the central Pacific Ocean and the South China Sea. Both surface water and water at the level of the pycnocline were sampled. Chemical extractions of the plastics recovered were analyzed for several organic pollutants and subsequent field and laboratory experiments were conducted to elucidate potential toxic hazards that plastics may pose to fish, seabirds, and other marine organisms.

Methods

Field Sampling

Sampling was conducted during the Third Joint US-USSR Bering & Chukchi Seas Expedition to the two seas and the central Pacific Ocean, along the segment from Hawaii to Singapore. Trawls for plastics were made from 15 September to 30 October 1988, along the 18,400-km cruise track of the Soviet R/V *Akademik Koroley*. During the cruise, the vessel

spent 8 days at Caroline Atoll, Kiribati, a remote coral atoll at 9°59.09'S, 150°14.04'W. Neuston sampling of the lagoon water of Caroline Atoll was done using a stationary 102 μ (0.5 \times 1 m) neuston net placed in the tidal currents of the entrance to the lagoon. The stationary net was left in position, with the opening facing toward the lagoon, over a 7-day period, during both flood and ebb tides. Also, one additional location in the central lagoon was sampled during two 30-min tows using two neuston nets (102 μ) towed alongside an inflatable boat.

Three different types of sampling methods were used in the open ocean. These included 1. surface sampling using a 1 \times 2-m tucker trawl (in the open position) equipped with a 94 μ net; 2. surface sampling with a 102 μ neuston net with a 0.5 \times 1-m opening; and 3. subsurface water sampling at the pycnocline horizon by deploying and hauling the tucker trawl in the closed position and fishing at depth in the open position. The pycnocline was determined using Soviet equipment installed aboard the research vessel to determine temperature, salinity, and density. Each net apparatus was equipped with a flow meter to determine the linear distance sampled that was later expressed on a surface area basis for surface sampling and a volume basis for sampling at depth.

Surface water trawls from the ship averages 15 min with half of the rectangular opening of each net below the surface. The tucker trawl was towed off the bow of the ship at speeds between 82.0 and 280.6 cm/s. Neuston trawls were done from the stern of the ship while drifting at speeds from 5.4 to 55.0 cm/s. At the end of each tow the sample was removed and passed through a series of acetone/hexane rinsed stainless steel sieves with pore sizes of 4 mm, 1 mm, 500 μ , and 106 μ to fractionate the sample. Each fraction was examined under magnification for the presence of plastics; marine organisms were separated from the sample for storage. Plastics recovered from the sample were immediately characterized as to size, type (raw pellet, fragments of plastic objects, fishing gear), and frozen in chemically-clean glass jars.

Chemical Analysis

All plastics (fragments and pellets) were removed from the fractionated sample, weighed, and extracted by shaking the sample three times in separate 5-ml rinses of hexane. Hexane extraction was used to remove nonpolar organics from the surface of the plastics and to avoid chemically dissolving the plastic samples. The extracts were combined and concentrated to a volume of 1 ml using a stream of dry nitrogen. Sample extracts were analyzed for chlorinated hydrocarbons using a Hewlett-Packard (HP)5890A gas chromatograph equipped with a ^{63}Ni electron capture detector and a 30m DBI column. An HP 5890A interfaced with an HP 5970 mass selective detector, in the full scanning mode from 50 to 450 atomic mass units, was used to detect the presence of other halogenated hydrocarbons and petroleum hydrocarbons.

Plastic Adsorption and Chemical Release Experiment

To assess the possible chemical hazards of plastic to marine life two experiments were conducted. These experiments were designed to evaluate the potential adsorption of organic

compounds from surface water and to determine if the gastrointestinal environment of birds could cause the release of organic compounds from raw polyethylene pellets.

To determine the adsorption potential of plastics from surface water, 100 g of new polyethylene pellets were placed in a 1-m-diameter brass-wire mesh enclosure in Baltimore Harbor, Chesapeake Bay. After 24 h, the pellets were collected, handled, and analyzed according to the procedures described above. At the same time the plastics were collected, a sample of the surface microlayer was collected by contact and adhesion of surface water to a glass plate. The plate was dipped repeatedly and rinsed with methylene chloride to obtain a sample volume of approximately 1-l of water from the microlayer. Water microlayer samples were extracted with methylene chloride and analyzed using the same methods as the plastic extracts. The purpose of the microlayer sample was to facilitate the comparison between compounds found in the surface microlayer and what was potentially adsorbed to the plastic pellets. This experiment was conducted to assess the possible adsorption characteristics of plastics under environmental conditions.

To determine if chlorinated or petroleum hydrocarbons could potentially be released from polyethylene pellets in the digestive system of birds, a simulation experiment was conducted. The experiment was patterned after those of Kimball and Munir (1971) using a 42 C HCl bath to simulate the physicochemical conditions in the digestive system of waterfowl. Hydrochloric acid was added to 1 N saline solution to yield digestive solutions with pH's of 1.4 and 2.8. Two 50-g samples of polyethylene pellets were added to glass jars containing either a 1 N saline only (controls), pH 1.4 solutions, pH 2.8 solutions, or a hexane (without saline). These solutions were agitated in a water bath at 42°C. At the end of 8 days, the plastics and the digestive solutions were extracted with methylene chloride and these extracts were analyzed for chlorinated and petroleum hydrocarbons using the methods described above.

Results and Discussion

Over 80,000 m² of surface water and 93,000 m³ of subsurface water were sampled during the course of the expedition (Table 1). The total number of stations sampled using either the 947 μ tucker trawl, the 102 μ neuston net, or both at a single location was 28 and 8 for the Pacific Ocean and South China Sea, respectively. Sampling at Caroline Atoll was done at only two locations. Plastics were recovered from 21% of the sample collected in the Pacific Ocean; five of six positive samples contained opaque polyethylene pellets. The sixth sample contained plastic fragments, not raw pellets. The concentration of plastics at positive stations varied considerably, with a maximum of 0.18566 mg plastic/m² (Table 2). Although sampling was done along the cruise track from as far north as 10°N to as far south as 10°S, plastics were only recovered from stations near the 10°N latitude area (Fig. 1). Tar balls were found at only two of the stations sampled in the open waters of the Pacific (Table 1).

TABLE 1

Sampling information and recoveries of plastics from the central Pacific Ocean and South China Sea. Sampling was done from 15 September through 30 October 1988.

Geographic Region	Sample Type	Net Mesh(μ)	Volume(m^3) or Area (m^2) Sampled	Total No. Stations	Number of Sampling Stations with		
					Plastic Fragments	Plastic Pellets	Tar Balls
Pacific Ocean	Surface	947	39,214	23	5	5	2
		102	3,627	8	1	0	2
	Pycnocline	947	51,657	9	0	0	0
Caroline Atoll	Surface	102	21,571	fixed station	0	0	0
	Surface	102	2,508	2 trawls	0	0	0
South China Sea	Surface	947	15,213	8	7	2	2
		102	394	1	1	0	0
	Pycnocline	947	42,107	4	1	0	0

TABLE 2

Occurrence and concentrations of plastics from the central Pacific Ocean and South China Sea. Sampling was done from 15 September through 30 October 1988.

Geographic Range	Stations Sampled		Plastic ^a Concentrations (mg/m ²) at Positive Stations	
	No. of Locations ^b	No. w/ Plastics	Mean	Range
Pacific Ocean	28	6	0.07340	0.01309 - 0.18566
South China Sea	8	7	0.19478	0.00126 - 0.69632

^a Plastic includes pellets and fragments.

^b Several stations were represented by more than one sample.

In the South China Sea, seven of the eight different locations sampled had plastics present in the surface water, but only two of the seven had plastic pellets (Table 1). Most of the plastics found in this area consisted of synthetic fishing line and secondary, manufactured plastics in the process of breaking down. Plastic concentrations in the South China Sea samples were considerably greater than those found in the Pacific Ocean, with a maximum concentration of 0.69632 mg plastic/m² (Table 2). Although only two stations sampled had tar balls present, one of these samples contained hundreds of tar balls and 164 of these were greater than 4 mm in size.

Sampling of the lagoon water at Caroline Atoll was done at two locations, one in the central lagoon and the other at a fixed station at the entrance channel to the lagoon. At the fixed station, current flowed through the neuston net at an average

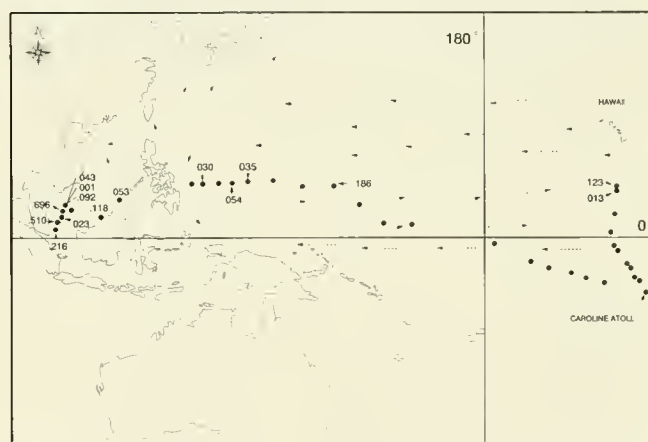


Fig.1. Locations sampled along the cruise track of the *Akademik Korolev*, September–October 1988. Sampling locations are indicated by solid dots. Plastic densities at positive stations are given in mg per meter square. Major currents for October 1988 are shown by the arrows.

velocity of 4.08 cm/s. No plastics or other anthropogenic materials were recovered from any of the samples at Caroline Atoll (Table 1).

The concentrations of plastics in the open Pacific Ocean stations that had plastics present in the surface water were below mean concentrations reported for the subtropical North Pacific (Wong *et al.*, 1974; Shaw & Mapes, 1979) and higher than from other studies in the North Pacific (Day & Shaw, 1987). Results from this study indicate that a much greater concentration of raw plastic pellets occur in the central Pacific compared to the North Pacific. There are no other data from the central Pacific region that can be used for temporal comparisons.

The greater frequency of occurrence of raw material plastic pellets compared to discarded plastic objects and tar balls in the South China Sea was somewhat surprising. The occurrence of discarded plastic may be expected from the

heavy shipping traffic in this region of the world. Moreover, there is extensive offshore oil production in the South China Sea and a high occurrence of tar balls would also be expected. The greater frequency of occurrence of plastic pellets compared to tar balls is noteworthy. The longevity of plastics in the marine environment likely contributes to the increase of this material in the oceans.

The distribution of plastics in the Pacific Ocean was largely a function of the major currents. All stations sampled that contained plastics were along a 10°N latitude convergence lying between the North Equatorial Current and the North Equatorial Countercurrent (Fig. 1). The most likely source of the plastics recovered at this convergence would either be from ships or as industrial waste from plastic-producing Pacific Rim countries.

All plastic sample extracts were analyzed for the organic compounds listed in Table 3. None of the samples contained quantifiable concentrations of organochlorine pesticides, PCB's, aliphatic hydrocarbons, or polycyclic aromatic hydrocarbons included in the analyses. The absence of detectable levels of these contaminants suggests that the plastics that were collected at sea did not adsorb any of these compounds, either because the plastic surface did not facilitate this or because the contaminants were not present in sufficient concentrations.

In the field experiment conducted in Chesapeake Bay's Baltimore Harbor, plastic polyethylene pellets left floating in the water for 24 h were extracted and analyzed using the same

methods as those collected at sea. A sample of the microlayer was taken the same time these plastics were placed in the water and was analyzed for the same contaminants as the plastic extracts. Two aromatic compounds, pyrene and fluoranthene, were detected in the microlayer sample; however, only fluoranthene was present in the extract of the polyethylene pellets.

These data indicate that polyethylene pellets have the potential to adsorb at least one organic compound, fluoranthene, from ambient seawater. The specific mechanism of adsorption could be either a binding of the organic compound to the plastic surface directly or to a film of water surrounding the plastic pellet. It is possible that other contaminants, especially those occurring in high concentrations in the microlayer, could also be adsorbed to floating plastic debris. Therefore, a potential for the transfer of certain organic pollutants from plastics to organisms that ingest them does exist. Plastics may serve as a vehicle for pollutant transport that may enhance exposure of organisms; however, if plastics also concentrate contaminants from the water this would result in an even greater hazard to marine organisms.

The other aspect of chemical-induced toxicosis resulting from plastic ingestion is that of the potential release of chemicals from the plastic to the organism. In the second experiment, none of the extracts of the acidic digestive solutions, or the hexane extraction of plastic pellets contained quantifiable concentrations of any of the hydrocarbon contaminants. These data suggest that even when exposed to mild heat, acids, and hexane, polyethylene pellets did not release appreciable quantities of chemicals. However, plastics subjected to real avian digestive systems would also be exposed to digestive enzymes and for possibly much longer periods of time. Ryan (1988b) found that domestic chickens fed polyethylene pellets retained 98.3% of them over an 18-day period. Moreover, there are many types of plastics and additives to plastics that could potentially be released during digestive processes in marine vertebrates.

Results of this study show that raw material plastic pellets are becoming increasingly more common in areas of the Pacific Ocean far removed from industrial sources. Although tar balls were once considered more common and widely distributed than marine plastics, their occurrence in the present study was less than that of plastics even in areas where oil development and tanker traffic is heavy. Plastic pellets do have the potential to adsorb certain organic contaminants from seawater; however, the types of compounds that can be adsorbed and possibly concentrated is not well understood. Polyethylene pellets subjected to conditions simulating the avian digestive system did not release detectable levels of chemicals. However, other types of plastics, and those that contain additives, were not tested.

Clearly, fish, seabirds, and other marine organisms will continue to be exposed to plastics at increasing rates. Regulations prohibiting ocean dumping of plastics have already been enacted; however, recycling, waste management, degradable plastics, and other alternatives must continue to be developed and implemented to abate the global problem of plastics in the oceans of the world.

TABLE 3

Organic compounds included in the analysis of extractions of plastics.

Chlorinated Pesticides and PCB's	Aliphatic Hydrocarbons	Polycyclic Aromatic Hydrocarbons
Heptachlorepoxyde	n - dodecane	Naphthalene
Oxychlordane	n - tridecane	Fluorene
Trans - chlordane	n - tetradecane	Phenanthrene
Cis - chlordane	n - pentadecane	Anthracene
Trans - nonachlor	Noncyclohexane	Fluoranthrene
Cis - nonachlor	n - hexadecane	Pyrene
Dieldrin	n - heptadecane	1,2,-benzanthracene
Endrin	n - octadecane	Chrysene
p,p' - DDT	n - nonadecane	Benzo(b)fluoranthene
p,p' - DDD	n - eicosane	9,10- diphenylanthracene
p,p' - DDE	Tetramethyl- pentadecane	Benzo(e)pyrene
PBC (1254)		Benzo(a)pyrene 1,2,5,6- dibenz- anthracene Benzo(g,h,i)perylene Perylene

The lower limit of quantification was 0.05 µg/g for aliphatic hydrocarbons, 0.4 µg/g for polycyclic hydrocarbons, 0.05 µg/g for chlorinated pesticides, and 0.25 µg/g for PCB's based on a 0.2 g sample.

This project was part of the First Joint US-USSR Central Pacific Expedition aboard the Soviet Research Vessel, *Akademik Korolev*. We express our appreciation to the US Fish and Wildlife Service, USA, and the State Committee for

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2.6 The Role of Solar Irradiation in the Oxidative Transformation of Benzo(a)pyrene

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Introduction

Organic pollutants entering water bodies, including the oceans, contain a wide range of substances. Some of these are quite easily subjected to degradation under the action of natural agents, while many other compounds are stable and persist in various compartments of the ecosystem. Among the persistent compounds are the carcinogens belonging to the polycyclic aromatic hydrocarbon (PAH) group. It has been established that PAH's enter the ocean in several ways, emissions into the atmosphere as a result of incomplete combustion of fuels, spillage during transportation of oil, and so forth. On the other hand, it is known that there exists a natural occurrence of PAH's (natural background) in the oceans. It is the view of several researchers (Tsyban, 1975; Izrael, 1984; Kirso *et al.*, 1988) that the main mechanism of self-purification of the hydrosphere from carcinogenic PAH's is biological (bacterial) oxidation. However, there are also other mechanisms for removal, including photooxidation under solar irradiation (Mill *et al.*, 1981; Bockris, 1982). It may be assumed that this process plays a significant role, especially in the surface water layer where the content of soluble oxygen is near 100% saturation (i.e., 10^{-3} mol/l). There are numerous factors that modify this process, including the physicochemical characteristics of water (turbidity, transparency, and the presence of other compounds) and the air above the sea surface (condition of the atmosphere, i.e., environment and weather conditions). Figure 1 illustrates the characteristic sunlight spectra at the sea surface (Ranby & Rabek, 1978). Photochemical reactions in the marine environment are also moderated by the level of atmospheric pollution with aerosol particles and smoke, as well as changes in ozone and other impurities. Solar irradiation at wavelengths less than 285 nm is to a large extent absorbed by ozone in the upper layer of the atmosphere. Therefore, the active spectra for this process are usually at wavelengths greater than 285 nm. Variations in the characteristics of the ozone layer therefore influence all the photochemical processes occurring on the oceans' surface.

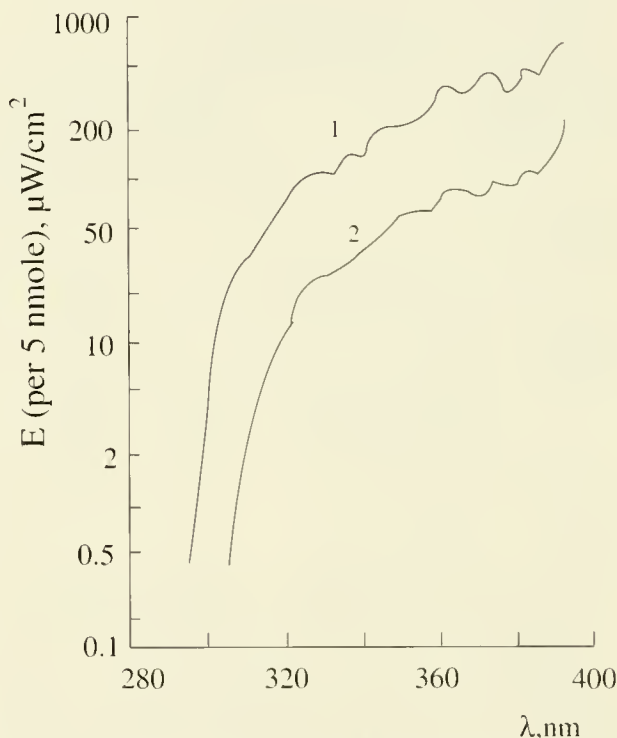


Fig. 1. Seasonal variations in solar spectra at the sea surface. 1 = July, 2 = December, E = Spectral Energy; λ = Wavelength (Ranby & Rabek, 1978).

The extent of these processes and their contribution to self-purification of the marine environment from carcinogenic PAH's are determined by both the value and distribution of solar irradiation energy (Mill *et al.*, 1981; Rabek, 1985) and the level of pollution of seawater, as well as the concentration and composition of pollutants. The latter may have an influence upon the pattern and intensity of the degradation processes of PAH's (Kirso & Gubergrits, 1971; Gubergrits *et al.*, 1975). Although systematic studies have been carried out on the photooxidation of individual PAH's in water (Kirso *et al.*, 1971; Gubergrits *et al.*, 1975; Paalme *et al.*, 1976, 1983), there are few data on these processes under natural conditions.

Therefore, during the cruise of the R/V *Akademik Korolev* (July–November 1988), a study was undertaken on the kinetics of the oxidative photolysis of a typical carcinogenic PAH—benzo(a)pyrene (BaP)—(Clar, 1971) in the Bering Sea and the tropical waters of the Pacific (Table 1).

It is known that the Bering Sea is almost wholly in the subarctic zone, excluding its northern parts, which are in the arctic temperature zones (Izrael & Tsyban, 1987). The main body of its waters is characterized by a subarctic structure whose specific feature is the existence of cold and warm intermediate layers. The upper layer thickness average 25–50 m, the salinity being 32.8–33.4‰ and the temperature, about 5 to 7°C. According to Izrael and Tsyban (1987), PAH's are permanent and typical components of these ecosystems.

TABLE 1

Exposure of BaP solution in seawater (the 47th cruise of the R/V *Akademik Korolev*).

Month (1988)	Exper. Number	Coordinates	Water Temp. t=°C	Average dose of solar radiation Q MJ/m ² during the first 3 hours
August	1	53°58'N/176°28'W	14.1	1.48
	2	53°58'N/176°28'W	15.7	1.09
September	3	09°54'S/156°23'W	26.4	3.50
	4	04°02'S/154°07'W	27.0	3.09
	5	09°59'S/150°15'W	27.0	4.90
	6	09°00'S/150°00'W	27.0	3.67
October	7	09°00'S/150°00'W	27.0	2.70
	8	09°00'S/150°00'W	27.0	3.00

Taking into account the low influence of this area from human activities, the physicochemical parameters of the atmosphere above these waters and characteristics of the surface water layer, a study of sunlight photolysis of PAH's in seawater at lower temperatures and low intensity of solar irradiation was of interest. The same experiment was carried out under tropical conditions—that is, at higher temperatures and considerable insolation with a salinity of 35.4‰.

Methods and Materials

The surface water samples taken at a depth of 0 to 0.5 m were sterilized by autoclaving for 2 h, cooled, and filtered through many layers of sterilized cloth into a sterilized dish. The BaP solution in seawater was prepared in 5-l glass cylindrical reactors whose sides were covered with black paper (water column height 20 cm). Benzo(a)pyrene was introduced as an ethanol solution (ethanol content up to 0.012%) by constantly mixing with a magnetic stirrer for 15 minutes. The BaP concentration was varied from 0.7 to 6.6 nanomoles (nm).

This solution was exposed to sunlight at the temperatures of the surface water for each given region. Simultaneously, the total solar irradiation dose, Q (MJ/m² per h), was measured pyranometrically (Table 1). The experiments were carried out with the following solutions:

- BaP solution in seawater;
- BaP solution in sterilized seawater; and
- BaP solution in sterilized seawater protected from light by black paper (autooxidation).

The exposures lasted for approximately 3 h in the first half of the day. The solutions were periodically sampled and the BaP concentration measured by chromatography techniques.

Conditions of analysis were as follows:

A 'Jasco' HPLC chromatograph (Japan), a fluorimetric detector, $\lambda_{ex} = 295$ nm, $\lambda_{em} = 408$ nm, solvent methanol–water (95:5) isocratic regime, eluent flow-rate 0.7 ml/min using a 25 × 0.25 cm ODS column, sample volume was 100 μ l.

Statistical kinetic data processing was performed using the least-squares method.

Results and Discussion

From kinetic data (Figs. 2–5, Table 2), it follows that during the first hour of exposure, a decrease in the BaP concentrations in seawater is described by a formal-kinetic equation for the first-order reaction where c_0 and c_t are the initial BaP concentration at zero time, and that at a certain time t , k is the constant of the first-order reaction, the dimensions for this constant are per second (s^{-1}).

$$\ln(c_0/c_t) = kt$$

The rate constant values obtained for the Bering Sea areas, the tropical part of the Pacific and the Caroline Atoll (Table 2) are of the same order as those found (Mill *et al.*, 1981) by photolysis of BaP in water ($\lambda = 366$ nm, BaP concentration 5×10^{-8} M, $t^\circ = 22$ – 28°C , $k = 3.86 \pm 0.71 \times 10^{-4} s^{-1}$). The half decay time of BaP under these conditions was 0.69 h. In our experiment the average rate constant value per unit Q was $(1.1 \pm 0.1) 10^{-4} s^{-1}$.

Irrespective of the areas under study and the sterility of water in those treatments that were subjected to photolysis (Table 2), the initial stage of the process, as mentioned above, is well described by an equation for the first order kinetics. At the same time, according to experimental data (Figs. 2–4), the oxidation of BaP in seawater without sunlight (autooxidation) for the Bering Sea areas and the tropical part of the Pacific is described by a formal-kinetic of a second-order type ($r = 0.90$ – 0.98). The rate constant value of BaP autooxidation in the Bering Sea water at a concentration of 5×10^{-8} M (July, $t^\circ = 21^\circ\text{C}$, $Q_{rel} \sim 0.68$ MJ/m² per h) was $(0.4 \pm 0.01) 10^4 M^{-1} s^{-1}$, but in the tropical part at a concentration of 1.7×10^{-8} (October $t^\circ = 27^\circ\text{C}$, $Q_{rel} \sim 3.00$ MJ/m² per h) $(9.08 \pm 1.90) 10^4 M^{-1} s^{-1}$, respectively.

TABLE 2

Kinetic characteristics of photochemical transformation of BaP in seawater under solar irradiation in the following areas:
 (a) the Bering Sea
 (b) the tropical part of the Pacific
 (c) the Caroline Atoll
 (47th cruise of the R/V *Akademik Korolev*, July–November 1988).

Experiment No. See Table 1	Initial BaP concentration $M \cdot 10^{-8}$	Rate constant $10^{-4} s^{-1} (k \pm n)$	Number of data points	Correlation coefficient r (first-order)	Sterility of media
(a)					
1.	1.47	1.69 ± 0.13	5	0.99	-
2.	4.20	1.60 ± 0.08	7	0.99	+
	4.44	1.20 ± 0.16	6	0.97	-
(b)					
3.	6.59	2.84 ± 0.48	5	0.96	+
	2.85	2.85 ± 0.98	4	0.90	-
4.	2.06	1.60 ± 0.49	4	0.92	+
(c)					
5.	1.90	2.99 ± 0.70	4	0.95	-
	2.14	4.05 ± 0.51	4	0.98	-
6.	0.70	4.20 ± 0.11	4	0.99	+
7.	11.10	8.77 ± 0.23	4	0.99	-
8.	2.00	3.67 ± 0.27	6	0.99	-

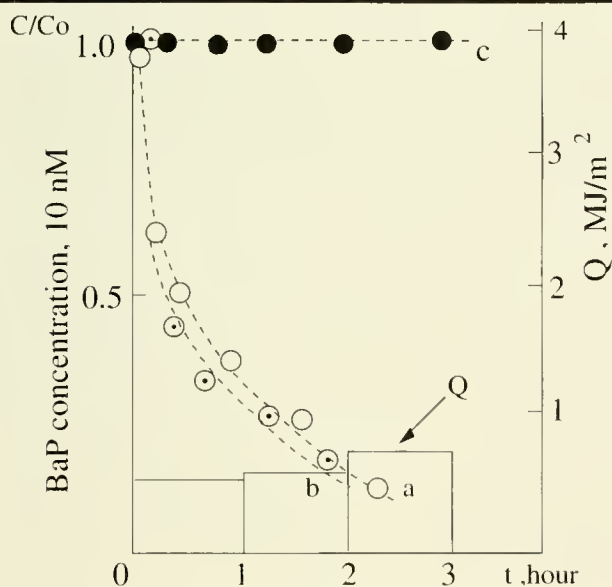


Fig. 2. Kinetics of BaP degradation under sunlight irradiation at the surface of the Bering Sea (coordinates: $67^{\circ}42'N$ $115^{\circ}43'W$): a) in sterilized seawater; b) in non-sterilized seawater; and c) by autoxidation (w/o light).

Thus, in the areas of exposure the rate constant values of BaP autoxidation in seawater differed within one order of magnitude. The shape of the kinetic curves (Figs. 2–4) also gives evidence of a negligible decrease in BaP concentration over time without sunlight.

While in laboratory experiments by photo-initiated UV-irradiation within a relatively wide wavelength range—around 200 nm—and a high oxygen atmosphere in a liquid medium, the degradation of BaP did not change until the

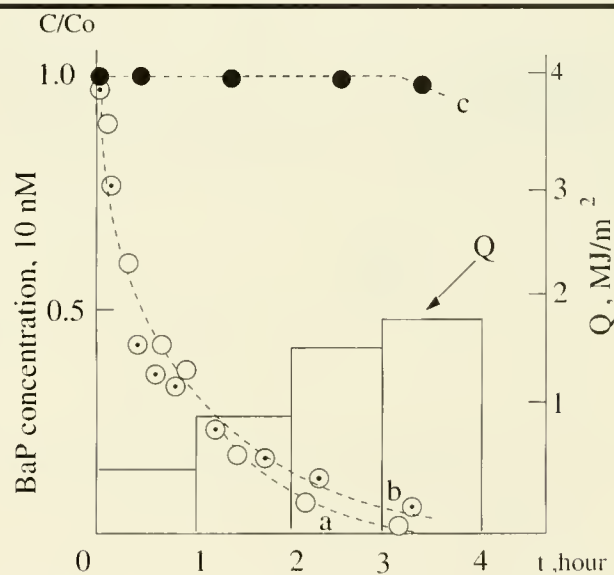


Fig. 3. Kinetics of BaP degradation under sunlight irradiation at the surface of the Bering Sea (coordinates: $53^{\circ}58'N$ $175^{\circ}28'W$): a) in sterilized seawater; b) in non-sterilized seawater; and c) by autoxidation (w/o light).

disappearance of the initial substance (zero-order reaction) (Gubergrits *et al.*, 1975; Paalme *et al.*, 1983). Under natural conditions in water (i.e., by sunlight photolysis), a decrease in the reaction rate is observed after the first hour of exposure (Figs. 2–5). This is especially noticeable in the Bering Sea area (Figs. 2–3). From the graphs (Figs. 2–5), it follows that the BaP half-decay times ($t^{1/2}$) in the Bering Sea waters were not less than 1 h, but in the tropical part of the Pacific, they were 0.6 h. The initial rate constant value of sunlight photolysis of BaP in the tropical zone water averaged $8.9 \times 10^{-12} \text{ mole s}^{-1}$, exceeding

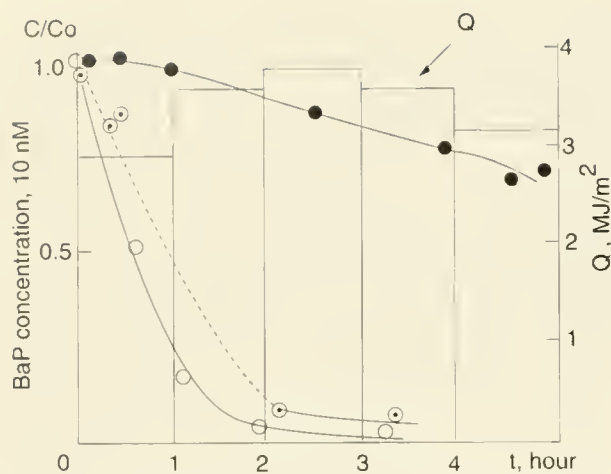


Fig. 4. Kinetics of BaP degradation under sunlight irradiation in the tropical part of the Pacific (coordinates: 09°54'N 156°23'W): a) in sterilized seawater; b) in non-sterilized seawater; and c) by autooxidation (w/o light).

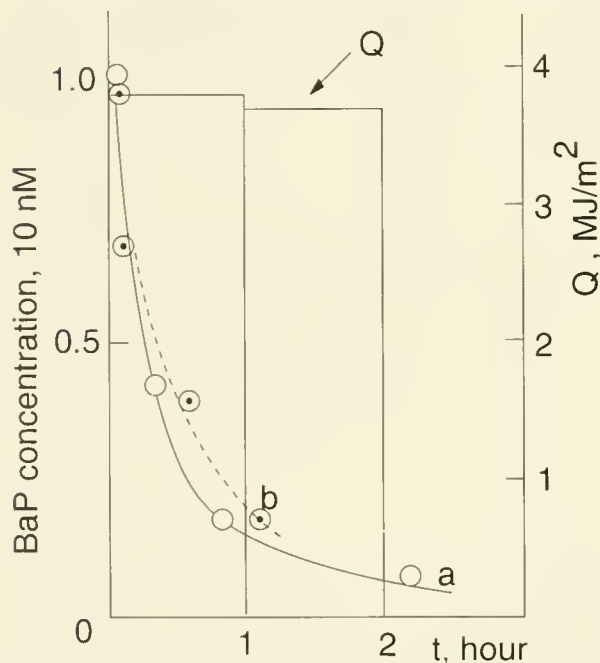


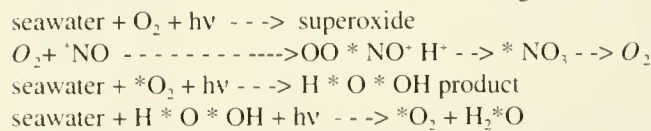
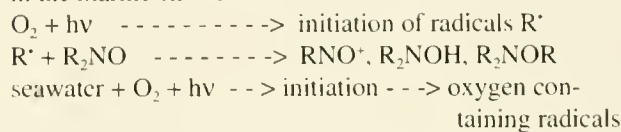
Fig. 5. Kinetics of BaP degradation under sunlight irradiation in the lagoon of the Caroline Atoll (coordinates: 09°54'N 156°23'W): a) in sterilized seawater; b) in nonsterilized seawater; c) by autooxidation (w/o light).

by $\times 3$ the rate for the Bering Sea area at similar initial BaP concentrations (2.44×10^{-12} mole s^{-1}). For comparison, it may be pointed out that at the initial concentrations of 10^{-9} M, the initial rate of sunlight photolysis of BaP in the Caroline Atoll is much higher than that found for BaP autooxidation in water under laboratory condition 1.67×10^{-12} and 0.3×10^{-12} mole s^{-1} , respectively (Kirso *et al.*, 1983).

Thus, experimental data, as expected, gave evidence of a dependence of BaP degradation on the location of exposure, intensity of solar UV-irradiation, and temperature of the environment, and data agreed well with the results obtained by Graupera and associates (Graupera *et al.*, 1988). Obviously, during photolysis of BaP by sunlight in seawater, the existence of microimpurities, inorganic components, salinity, and general

water composition all have a major impact on photochemical reactions in different areas of the world oceans. A comparison of experimental kinetic parameters and literature data (Mill *et al.*, 1981) suggests that proceeding from the values of k at $T^{1/2}$ of BaP under similar conditions of its photolysis in water ($\lambda = 366$ nm and concentration of 5×10^{-8} M) the value of quantum yield ϕ_{exp} (the number of molecules subjected to transformation as a result of adsorption of one energy quantum) is almost equal to $\phi = 5.4 \times 10^{-4}$ —that is, less than one (Mill *et al.*, 1981). Consequently, the processes under study are complex, involving competing chemical reactions. Thus, the degradation of BaP is initiated directly or indirectly and proceeds under solar irradiation.

Photochemical reactions were investigated with soluble oxygen in the presence of different inorganic and organic components in water bodies. Zafiriou (Zafiriou *et al.*, 1989) presented the following scheme for generation of free radicals in the marine environment:



According to (Mopper *et al.*, 1989) the concentration of high-energy (more than 4 kcal/mole) oxygen-containing radicals in seawater is low and makes for hydroxyl groups (OH)—for example, in subtropical coastal areas 11.9×10^{-18} M and for open sea 1.1×10^{-18} M, correspondingly. Consequently, it may be assumed that BaP (and other PAH's) is subjected to photodegradation due mainly to secondary photochemical reactions with different reactive radicals formed directly under the action of light quanta or indirectly (see the scheme). According to our results, the rate of BaP transformation depends primarily on the sunlight intensity. Obviously, then, the mechanism of photochemical oxidation of organic xenobiotics of the PAH type is not different in northern and southern areas (i.e., the amount of oxidizing particles sufficient for transformation is generated whose excess favors the first-order reaction [pseudomonomolecular] relative to BaP).

A study of the influence of inorganic salts and microimpurities on the photochemical processes in the marine ecosystems requires further research.

To sum up, it should be pointed out that the experiments (under natural conditions) were carried out with only one reference PAH, benzo(a)pyrene, and in the marine environment many other PAH's are present (see Fig. 6). To estimate the reactivities of other PAH's undergoing photooxidation in seawater, the data obtained by Paalme *et al.* (1988) were considered. It appears that the rate of the process for individual homologs differs by factors of over 140 (Fig. 6). Anthracene and its derivatives are easily oxidized, while the more condensed systems—for example, coronene—remain more stable. It may be assumed that as a result of photochemical oxidation, the quantitative ratio of PAH's in the marine environment shifts toward the heavier homologs.

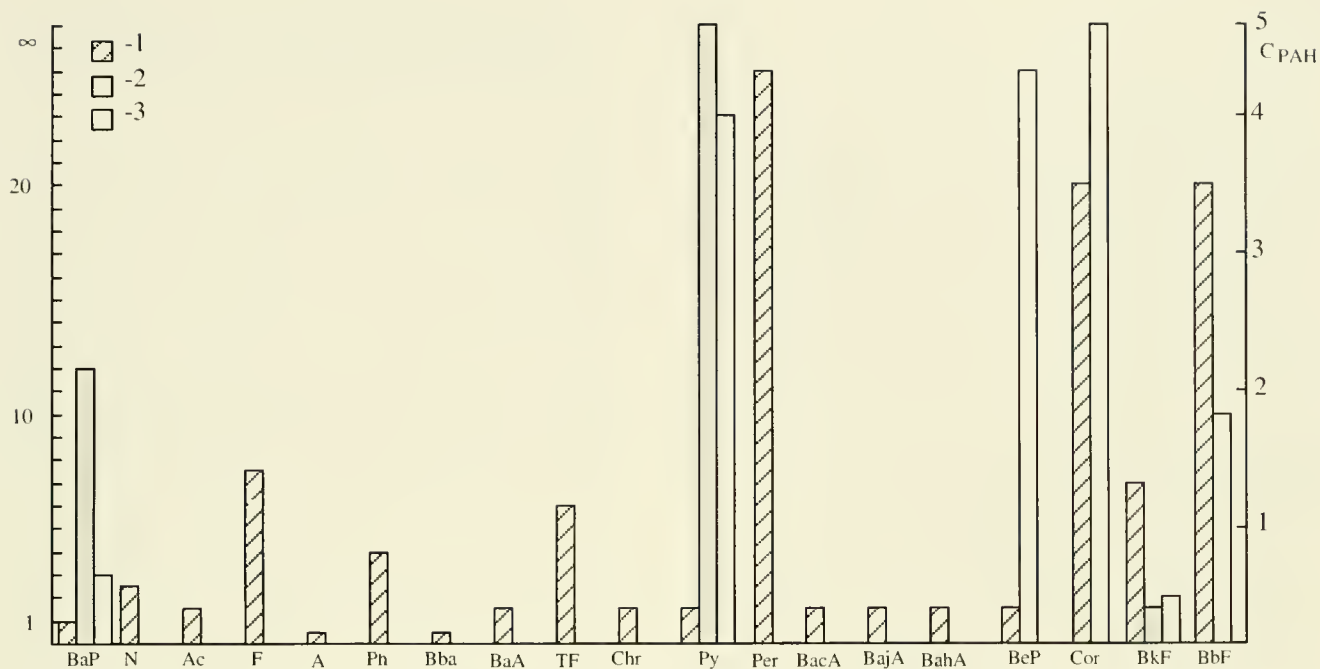


Fig. 6. Relative rates (v) of photoinitiated transformation of PAH's in water: (1) (Paalme *et al.*, 1983); and their content (ng/l) in the water of the Bering Sea; (2); and the Baltic; and (3) (Kirso *et al.*, 1989).

Thus, under conditions similar to natural ones (i.e., under sunlight), it has been shown that a certain amount of PAH's may be subjected to sunlight photolysis. The degree of BaP transformation in the experiments was governed by the intensity

of total sunlight irradiation in a given region and by the conditions of exposure (temperature, turbidity, etc.). Autoxidation plays an insignificant role in self-purification of the marine environment from BaP.

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Chapter 3:

BIOLOGICAL INVESTIGATIONS IN THE CENTRAL PACIFIC

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3.1 A Description of Bacterioplankton

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Introduction

An assessment of the role played by bacteria in biodegradation processes occurring in the World Ocean requires data concerning bacterial population counts, bacterial population distributions, and a number of other functional characteristics.

Studies carried out in the course of the First Joint US-USSR Central Pacific Expedition in the equatorial Pacific and the South China Sea produced new findings characterizing the present state of microbiocoenoses in this part of the World Ocean.

Materials and Methods

The microbiological studies described below were conducted using methods set out in several handbooks (Romanenko & Kuznetsov, 1974; Tsyban, 1980; Tsyban *et al.*, 1988). Analyses of total counts, biomass, bacterioplankton production, indicator group distribution, and degradation process rates were performed at 18 stations. The samples were taken from 6 to 19 depths using 5-l Niskin bottles. To allow for overall bacterial counts, samples of 20–50 ml were passed through “Synpor 8” membrane filters with pore size 0.23 μm . The filters were desalinated onto filter paper moistened with distilled water, dried, and dyed with a 5% carbolic erythrosine solution. The bacteria deposited on the filters were counted by direct oil-immersion microscopy ($\times 1350$ magnification, 20 visual fields).

The average bacteria volume was assessed by measuring bacterial cell size with the aid of an ocular ruler. The mean bacterial cell volume was found to be 0.3 μm^3 .

The daily bacterial biomass production rate was calculated on the basis of CO_2 assimilation in darkness. The latter was ascertained using a radiocarbon technique (Romanenko, 1964; Sorokin, 1971a). The determinations were made in 100–120-ml jars. The radioactivity of the working solution of carbon-labeled sodium carbonate introduced into the sample-containing jars was 18×10^6 counts/min. The samples were incubated in darkness for 24 h at the temperature of the water where the sample was taken. Once the incubation was completed, the samples were fixed with a 40% formaldehyde solution, then passed through “Synpor-7” filters (pore size 0.35 μm). The radioactivity of the bacteria deposited on the filters was measured using an “Intertechnique” liquid scintillation counter. The scintillation cocktail was ZhS-8. The CO_2 assimilation rate in darkness (T_{ass}) for the bacterial plankton was calculated by means of the formula

$$T_{\text{ass}} = \frac{r \times C_{\text{carb}}}{R \times t},$$

where r — the radioactivity of the bacterial cells on the filter (counts/min);

C_{carb} — the hydrocarbonate content of seawater (mg/l) determined by direct titration of 0.1N HCl in the presence of methyl red;

R — the radioactivity of the isotope $\text{Na}^{14}\text{CO}_3$ used in the experiment (counts/min);

t — the incubation time (h).

The bacterial biomass production was obtained by calculation, setting $P_b = T_{\text{ass}} \times 16.6$. Bacterial plankton respiration was determined by applying the formula

$$D = T_{\text{ass}}/7,$$

where D — the amount of oxygen expended on decomposition ($\text{mg l}^{-1} \text{d}^{-1}$);

T_{ass} — rate of CO_2 assimilation in darkness (μg of C per $\text{l}^{-1} \text{d}^{-1}$); and

the coefficient of 7 is the ratio of oxygen uptake to CO_2 assimilation.

The studies were carried out in the tropical and equatorial portions of the Pacific Ocean, as well as in the South China Sea. The locations of the stations are indicated on the Frontispiece.

Results

The equatorial Pacific is characterized by upwelling. The latter occurs mostly along the boundaries of west-to-east zonal flows and alternates with surface-water downwelling zones. The intrusion of deep waters rich in biogenic elements into the euphotic layer determines the way in which biocoenoses develop (i.e., their spatial and trophic structures, productivity, and other functional characteristics) (Vinogradov, 1978).

Some temperature stratification was evident during the period of our studies in the 0–8°N, 160–180°E rectangle of the equatorial Pacific. The water temperature and dissolved oxygen content remained virtually constant down to a depth of 150 m. The parameters in question declined rapidly below this level, however, which necessarily affected the formation and distribution of microbiocoenoses. Results of analyses (Figs. 1–3) indicate that bacterioplankton counts and biomass in the 0–100-m layer varied within fairly broad limits. The highest bacterial population density was noted at Station 116, where the average total count and biomass were 591×10^3 cells/ ml^{-1} and $13.29 \mu\text{g C l}^{-1} \text{d}^{-1}$, respectively. The lowest bacterioplankton concentration was noted at Station 118, where the average total bacteria count was 199×10^3 cells/ ml^{-1} and the biomass $4.48 \mu\text{g C l}^{-1} \text{d}^{-1}$. The average values of the total bacteria count and biomass in

the 0–100-m layer of the equatorial Pacific were 360×10^3 cells/ml⁻¹ and $8.10 \mu\text{g C l}^{-1} \text{d}^{-1}$, respectively. Such a level of development of bacterioplankton and its biomass is typical of the bacterial population density in the euphotic zone with background upwelling (Sorokin, 1978). According to data reported in the literature, the principal bacterioplankton count and biomass maxima in stratified tropical waters are usually situated at the upper boundary of the thermocline. The formation of the microbiocoenosis in this zone is attributable to the arrival of biogenic substances from lower layers, to the stable existence of the phytoplankton population in the euphotic layer, and to the stable existence of the phytoplankton population in the euphotic layer. This in turn ensures that the bacterioplankton receives a steady and readily assimilable supply of organic matter (Sorokin, 1971b, 1982).

According to our observations, the vertical distribution of microflora (Figs. 1–3) included several regularly observed maxima occasioned by the delivery of labile organic matter to the zone of maximum phytoplankton synthesis. These lay at 15–25 m for Stations 115–117, at the upper boundary of the thermocline (100–250 m), and at a depth of 1,000–1,500 m (Stations 118–120) (i.e., at the boundary of mixing of the Antarctic waters).

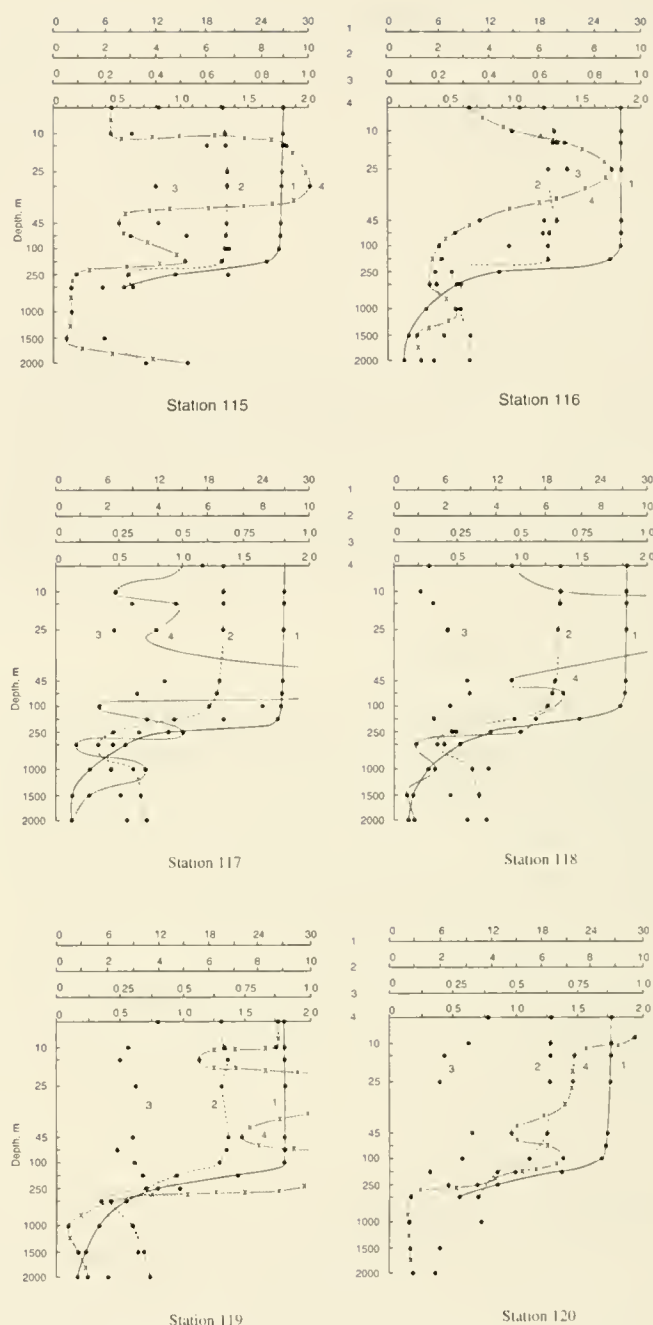
The principal bacterioplankton concentration maximum lay at a depth of 100 m. The microflora counts and biomass were, on the average, 1.3 times the corresponding values for the euphotic zone. The level of microbiocoenosis development in deeper waters (at depths of 1,000–2,000 m) was lower. The total bacterioplankton counts and biomass value here turned out to be lower than at the upper boundary of the thermocline by a factor of 1.5. The constraints limiting microfloral development in these deeper waters were very probably the lower temperature and high pressure.

There was a clearcut tendency for the bacterial population density in the 0.5–250-m layer to decrease in the east-to-west direction. Thus, the bacterioplankton counts and biomass at Stations 115 and 116, situated in the eastern part of the equatorial zone, were, on the average, twice as high as at Station 120, lying to the west of them. This observation was in keeping with the declining intensity of upwelling from east to west (Vinogradov, 1978).

Thus, total bacterioplankton counts and biomass in the waters of the equatorial Pacific, which have suffered less of an impact from human activities than other parts of the Ocean, are fully comparable with those observed for oligotrophic and mesotrophic waters.

As in the quantitative parameters, the functional characteristics undergo considerable change as one moves from east to west. Data obtained in the course of the present study made possible some quantitative assessments of certain functional characteristics of microbiocoenoses, such as microfloral activity, bacterial biomass production rate, and the rate of degradation of organic matter in the equatorial Pacific.

Analysis of the results (Figs. 1–4) shows that microfloral activity in the 0–100-m layer in the equatorial zone varied over a broad range and had a tendency to increase in the east-to-west direction despite the gradual diminution of bacterial population



Figs. 1–3. Vertical distribution of: (1) water temperature in °C; (2) dissolved oxygen in mg/l (3) total bacteria count in millions of cells/ml; and (4) CO₂ assimilation by bacteria in darkness, in g C l⁻¹ d⁻¹. All data refer to the equatorial Pacific.

density. Thus, the values for the amount of CO₂ assimilated by bacteria per day under conditions of darkness averaged 1.5–2.0 times higher for Stations 119 and 120 than for the more easterly Stations 115–116. Both bacterial biomass production and organic matter degradation also increased. Whereas the bacterial production values in the 0–100-m layer at Stations 115 and 116 averaged 15.2 and 16.6 $\mu\text{g C l}^{-1} \text{d}^{-1}$, the corresponding values at Stations 119 and 120 were 25.5 and 32.5 $\mu\text{g C l}^{-1} \text{d}^{-1}$. The respiratory uptake of oxygen by microorganisms in the western area was virtually double. The rate of organic matter degradation increased from 78.7 $\mu\text{g C l}^{-1} \text{d}^{-1}$ at Station 116 to

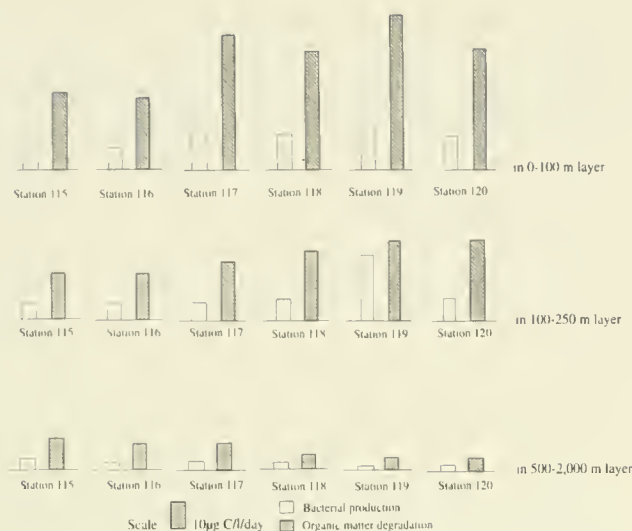


Fig. 4. Bacterial production and organic-matter degradation in the equatorial Pacific.

104.4 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ at Station 119. The average rate of bacterial organic matter degradation in the 0–100-m layer in this part of the Pacific equaled 75.5 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The P/B coefficient for microflora in the 0–100-m layer averaged 2.9, which was somewhat higher than the value previously obtained by Sorokin (1973). The average value of the P/D coefficient was 0.31.

Maximum microfloral activity in the 0–100-m layer occurred at a depth of 25 m. The rate of assimilation in darkness here attained a level typical of mesotrophic waters, averaging 1.94 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The respiratory oxygen uptake by microflora also showed peak values, averaging 0.28 mg/l—a finding that is in good agreement with that of Sorokin (1973). The rate of bacterial degradation of organic matter in the euphotic zone reached maximum levels on the order of 103.9 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ (Fig. 4).

The activity of microflora in the 100–250-m layer was somewhat lower compared with the euphotic zone. The rate of CO_2 assimilation in darkness averaged 1.10 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. Bacterial biomass production was lower than in the top layer by an average factor of 1.2. The bacterial degradation rate averaged 58.0 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The P/B coefficient was 2.2, the P/D coefficient, 0.31.

Bacterial activity diminished sharply at depths exceeding 250 m. The rate of bacterial biomass production in the 500–2,000-m layer was, on the average, almost five times lower compared with the upper layers of the water column, ranging from 2.5 to 5.5 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ and averaging 4.2 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The bacterial degradation rate decreased more than fivefold compared with that of the euphotic zone. This decreased rate of degradation was clearly attributable to lower temperatures. The P/B coefficient in the 500–2,000-m layer was 0.7. The water column at 500–2,000 m was found to include two layers of heightened activity, one at 1,000 m, the other at 2,000 m. However, bacterial production and degradation rates in these maximum-activity layers did not attain the average values characteristic of the top layer.

The next transect lay along 10°N in the western Pacific (Frontispiece). The waters in this area exhibited lower productivity as compared with those of the equatorial portion of the central Pacific. The level of development of

microbiocoenoses at most of the stations corresponded to the upper limit of productivity for oligotrophic waters. The bacterial population density in the 0–100-m layer ranged from 129 to 545 $\times 10^3$ cells/ml⁻¹ (Figs. 5–7). The highest bacterioplankton concentration occurred at Station 123, where the average count and biomass reached 387 $\times 10^3$ cells/ml⁻¹ and 8.7 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The highest microfloral activity was observed at Station 121, where the rate of CO_2 assimilation by bacterioplankton averaged 1.76 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, which corresponds to the upper limit for oligotrophic waters. The lowest microfloral activity was noted at Station 122. The daily rate of CO_2 assimilation in darkness here was 3.4 times less than at the preceding station.

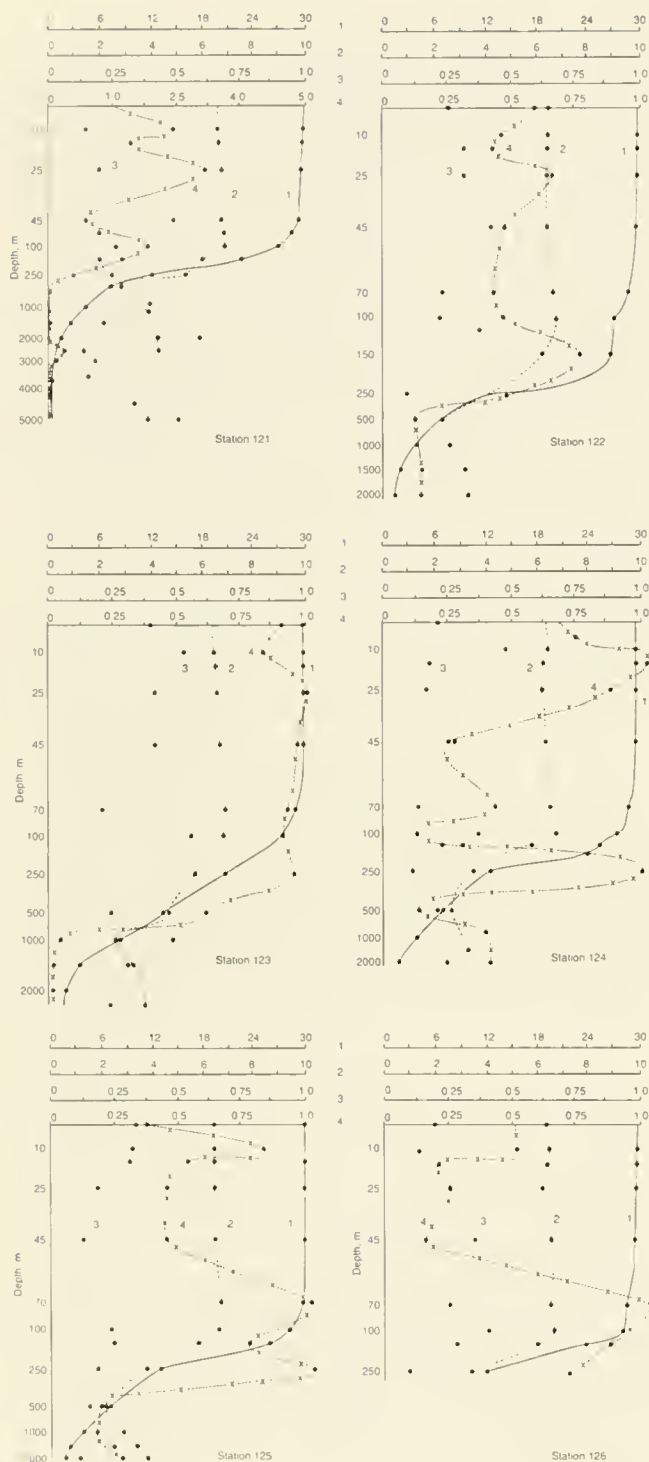
Bacterial biomass production in the 0–100-m layer ranged from 2.1 to 52 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ (Fig. 8). The oxygen uptake due to bacterioplankton respiration averaged 0.12 mg/l. The rate of organic matter degradation by bacteria lay in the 27–94 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ range, with an average value of 47 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The P/B coefficient was 2.3.

The portion of the water column lying below the thermocline (150–500 m) exhibited relatively low bacterial population levels. The total bacteria counts here ranged from 109 to 492 $\times 10^3$ cells/ml⁻¹, the biomass from 3.9 to 7.7 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The mean bacteria count and biomass for the 150–500-m layer turned out to be 237 $\times 10^3$ cells/ml⁻¹ and 5.3 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, respectively. The microfloral activity was somewhat lower than in the supernatant 100 m of the water column. The rate of CO_2 assimilation by bacteria in darkness ranged from 0.12 to 1.36 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, averaging 0.62 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The most intense microfloral activity occurred at Station 125, where the mean CO_2 assimilation rate reached 0.78 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The lowest rate of 0.47 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ corresponded to Station 122.

The bacterial biomass production rate turned out to be 1.5 times lower than in the 0–100-m layer. Oxygen uptake due to bacterioplankton respiration in the 150–500-m layer averaged 0.08 mg/l, indicating a relatively low rate of degradation. The degradation rate OB ranged from 25 to 42 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, with an average value of 33 $\mu\text{g C l}^{-1} \text{ d}^{-1}$.

A trend towards increased bacterial population densities was noted in the deeper (1,000–2,000 m) portion of the water column. For example, the total bacteria counts at 2,000 m for Stations 121 and 122 were much higher than further up the water column. Some increase in bacterioplankton concentrations was likewise noted at 1,500 m at Stations 123 and 125. The average total bacterial count and biomass for the 1,000–2,000 m layer was 281 $\times 10^3$ cells/ml⁻¹ and 6.3 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, respectively. These values were quite closely comparable with the data for the 0–100-m layer.

The results showed that microfloral activity in the deeper portions of the water column was suppressed by low temperatures and high pressures. The rates of CO_2 assimilation by bacteria in darkness for the 1,000–2,000-m layer ranged from 0.11 to 0.42 $\mu\text{g C l}^{-1} \text{ d}^{-1}$, averaging 0.22 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. Bacterial biomass production was, on the average, 2.8 times lower than in the 150–500-m layer. Oxygen uptake due to bacterioplankton respiration averaged 0.03 mg/l. The rate of degradation of organic matter was minimal, the average value for the layer being 12 $\mu\text{g C l}^{-1} \text{ d}^{-1}$. The P/B coefficient was 0.5.



Figs. 5-7. Vertical distribution of: (1) water temperature in °C; (2) dissolved oxygen in mg/l (3) total bacteria count in millions of cells/ml; and (4) CO_2 assimilation by bacteria in darkness, in $\text{g C l}^{-1} \text{d}^{-1}$. All data apply to the western Pacific.

The bacterioplankton distribution over the water column in the western Pacific exhibited some temperature stratification, with several bacterial population and activity maxima present (Figs. 5-7). Three bacterioplankton concentration peaks were quite clearly in evidence: the first one lay below the zone of maximum phytoplankton synthesis at a depth of 45 m, the second above the upper boundary of the thermocline at a depth of 100 m, and the third at 1,500 m. Elevated microfloral activity was noted in the euphotic zone (10-15 m), above the

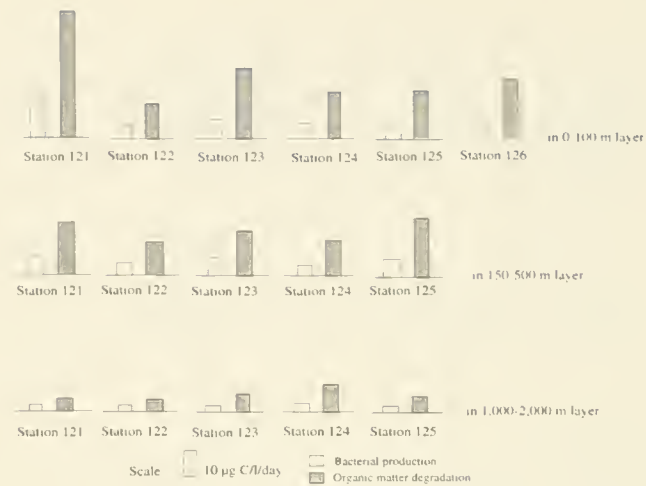


Fig. 8. Bacterial production and organic-matter degradation in the western Pacific.

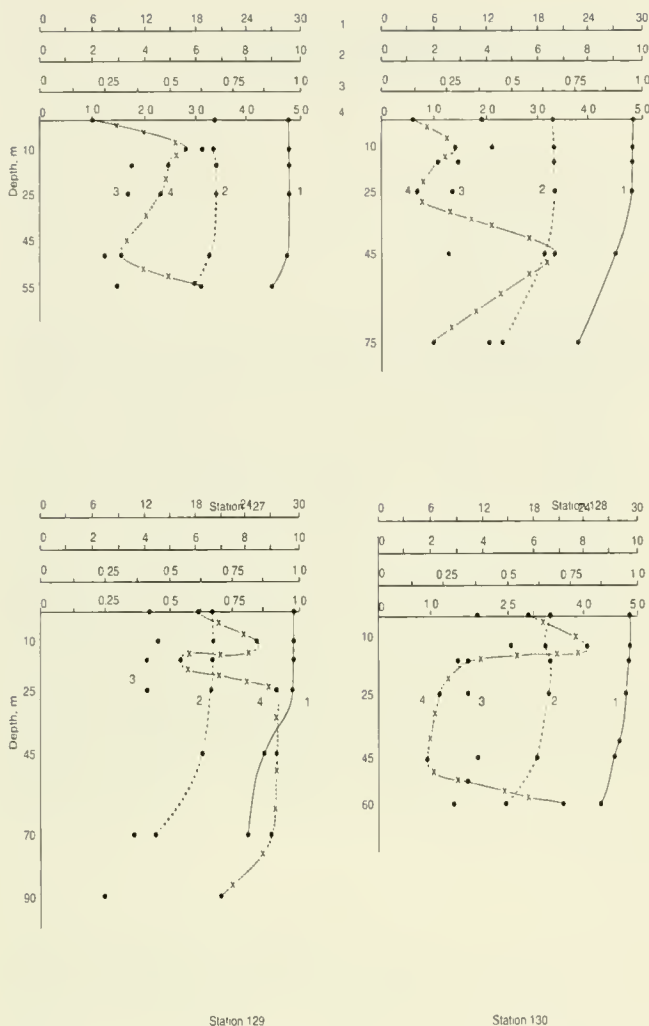
thermocline, and at a temperature drop boundary. This behavior of bacterioplankton distribution and activity over the water column was closely related to water dynamics and was typical of the oligotrophic waters of the tropical oceans.

The next series of studies was conducted in the South China Sea, whose waters are more polluted than those of the central Pacific. Analyses of total biomass, bacterioplankton production, and bacterial degradation were performed at five stations. The results of the measurements are presented in Figs. 9-11. These show that the bacterioplankton count in the euphotic layer (0-50 m) ranged from 176 to 611×10^3 cells/ ml^{-1} . The highest bacterial population densities were noted for Stations 130 and 131, situated in coastal waters; the lowest values were obtained at pelagically situated Station 127. The bacterioplankton count at certain levels of the water column attained 611×10^3 cells ml^{-1} . The average bacterioplankton count in this area equaled 354×10^3 cells/ ml^{-1} .

The bacterioplankton biomass varied over a broad range of values from 3.16 to $11.81 \mu\text{g C l}^{-1} \text{d}^{-1}$. Data for the 0-50-m layer averaged for individual stations yielded values from 6.67 to $9.16 \mu\text{g C l}^{-1} \text{d}^{-1}$. Mean data for bacterioplankton biomass and counts for the euphotic zone place the investigated portions of the South China Sea in the oligotrophic category.

Low bacterioplankton counts notwithstanding, microfloral activity was relatively high. Thus, the rate of CO_2 assimilation by bacteria in darkness ranged from 0.52 to $4.07 \mu\text{g C l}^{-1} \text{d}^{-1}$, averaging $1.60 \mu\text{g C l}^{-1} \text{d}^{-1}$ for all the areas studied. Bacterioplankton production for individual stations ranged from 12.8 to $39.7 \mu\text{g C l}^{-1} \text{d}^{-1}$ (Fig. 11). The value for the entirety of the area investigated was $26.6 \mu\text{g C l}^{-1} \text{d}^{-1}$.

The rates of bacterioplankton respiration in the 0-50-m layer calculated as averages for particular stations ranged from 0.11 to $0.34 \text{ mg O}_2 \text{ l}^{-1} \text{d}^{-1}$. The range of bacterial respiration rates for individual samples ranged from 0.07 to $0.58 \text{ mg O}_2 \text{ l}^{-1} \text{d}^{-1}$. The maximum bacterioplankton respiration rate was observed at Station 130, the minimum at Station 129. The average daily oxygen uptake by bacterioplankton in the area was 0.23 mg/l^{-1} , which was in good agreement with values calculated from experimental data on the respiration of the plankton community as a whole.



Figs. 9-10. Vertical distribution of: (1) water temperature in $^{\circ}\text{C}$; (2) dissolved oxygen in mg/l ; (3) total bacteria count in millions of cells/ml ; and (4) CO_2 assimilation by bacteria in darkness, in $\text{g C l}^{-1} \text{d}^{-1}$. All data apply to the South China Sea.

Total bacterial degradation in the water column at individual stations ranged from 41 to $127 \mu\text{g C l}^{-1} \text{d}^{-1}$. The average for a whole of the area studied was $86 \mu\text{g C l}^{-1} \text{d}^{-1}$.

The vertical distribution of bacterioplankton over the water column within the euphotic zone included a clearly evident peak at a depth of 10 m (Figs. 9,10). The mean bacterial density and biomass in this layer were $450 \times 10^3 \text{ cells/ml}^{-1}$ and $10.1 \mu\text{g C l}^{-1} \text{d}^{-1}$, respectively. Both counts and biomass then decreased with depth.

Microfloral activity varied considerably over the water column. Two microfloral activity peaks were observed at several stations: one lay at a depth of 10 m, the other at or near the sea bottom. Enhanced production-degradation activity was likewise noted at the corresponding depths. Bacterial biomass production in the peak-activity layers was 2.5 times the bacterial production obtained for the entire sea area studied. The degradation rate OB in the bottom layer was 3.5 times that noted for the surface layer.

Discussion

Particular portions of the Pacific Ocean exhibited differing levels of microbiocoenosis development. The equatorial Pacific and South China Sea areas are closely similar with respect to bacterioplankton and biomass parameters in their euphotic zones. On the other hand, the level of development of the bacterial population in the western Pacific was found to be much lower. The South China Sea exhibited relatively high microfloral activity. Values characterizing bacterial production and organic matter degradation in the sea were similar to those reported for the mesotrophic waters of the tropical ocean. The level of production-degradation processes in the western Pacific was almost half of that in both the equatorial ocean and the South China Sea and corresponded to values characteristic of oligotrophic waters.

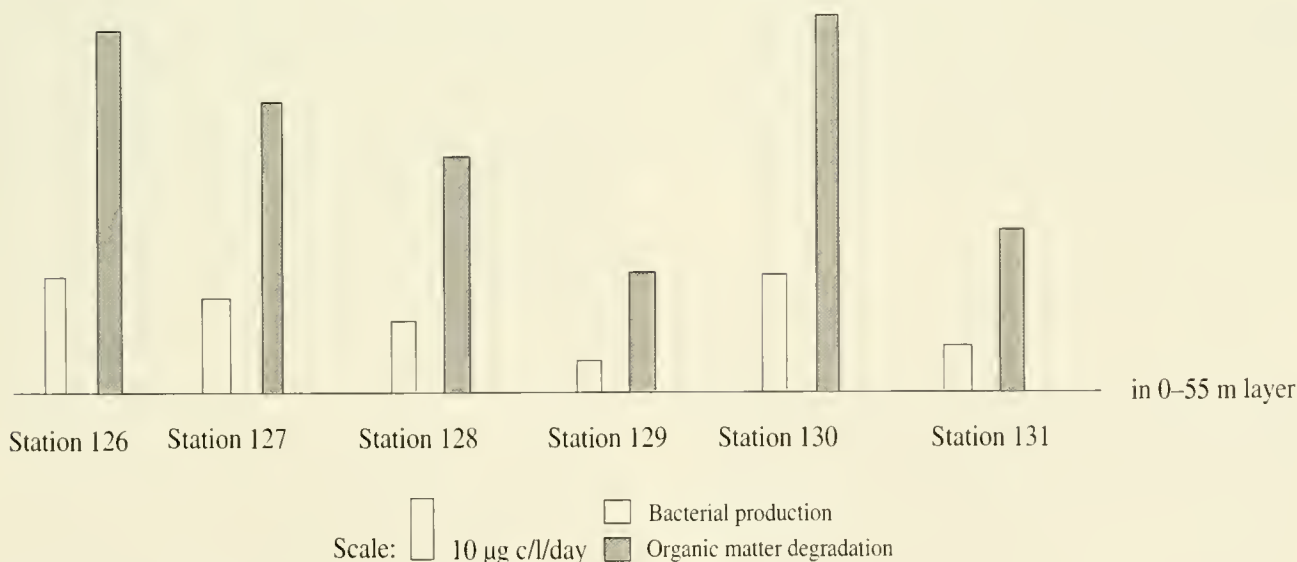


Fig. 11. Bacterial production and organic-matter degradation in the South China Sea.

3.2 A Study of Primary Phytoplankton Production

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Introduction

The study of the rate of formation of new organic matter by phytoplankton photosynthesis in the tropical Pacific reported in the present paper was carried out during the First Joint US-USSR Central Pacific Expedition aboard the R/V *Akademik Korolev* in 1988. The ocean areas investigated included portions of the central and western Pacific, which had received little previous attention. Primary production in the area of the first transect, beginning near Caroline Atoll and ending at Tarawa Island (Republic of Kiribati), ranges from values characteristic of oligotrophic parts of the ocean (100 mg C/m²/day and lower) to values corresponding in mesotrophic areas of the Pacific (25 mg C/m²/day) (Sorokin, 1976).

The central portion of the tropical Pacific (stations of the second transect) may be characterized as an oligotrophic productivity zone where a major role in primary production enhancement is played by synoptic phenomena such as cyclones, tornadoes, waterspouts, et cetera (Sorokin, 1976). Situated in the open portion of the northern tropical Pacific (i.e., within the northern tradewind zone), the second transect studied showed a primary rate of organic matter production by phytoplankton of about 100 mg C/m²/day (Sorokin, 1976). The relatively low rates of primary production in this part of the Pacific are attributable largely to the deficiency of biogenic elements in the photosynthetic layer. These low concentrations are in turn due to anticyclonic circulation, which produces downwelling of nitrogen- and phosphorus-poor surface waters. It is the resulting low nitrogen and phosphorus levels in the photosynthetic layer that limit photosynthesis rates in the phytoplankton community.

Despite the absence of significant seasonal variations in illumination and water temperature in the tropical ocean, considerable seasonal changes of photosynthesis rates have been reported in spring and autumn (Sorokin, 1976).

Materials and Methods

Studies at Stations 114–120 in the central tropical Pacific were conducted from 27 September to 7 October 1988. The work at Stations 121–126 along the Marianas transect was performed from 16 October to 21 October. Primary production was determined by means of a radiocarbon version of the “jars method” proposed by Sorokin (Sorokin *et al.*, 1983). Work at each station included measurements of photosynthesis in a surface-water sample (C_{ps}) as well as determinations of photosynthesis in the water layer as a function of phytoplankton distribution over the water column (the coefficients K_d).

The light curves (the coefficients K_d) were determined at one station in each transect. The sample incubation was usually 8–10 h, beginning in the morning. The radioactivity of filters with ¹⁴C-labeled phytoplankton and of the working NaH¹⁴CO₃ solutions was measured using a Nuclear Chicago “Mark 2” scintillation counter. Sample radioactivities were counted using liquid scintillator cocktails of previously described composition (Sorokin, 1976; Sorokin *et al.*, 1983).

Primary production was calculated using the standard formula, with a factor of 1.5 to correct for ¹⁴C loss due to phytoplankton sample filtering (Sorokin, 1976). All determinations of primary production were carried out in triplicate. The extent of the photosynthesis zone was taken to equal the white-disk transparency multiplied by three. Samples for determining phytoplankton production were taken using 5-l Niskin bottles at depths of 0.5; 10; 15; 25; 45; 70, and 100 m.

Results

The vertical structure of phytoplankton communities in high-transparency tropical ocean waters is characterized by several phytoplankton growth peaks or maxima in the euphotic zone, whose depth sometimes exceeds 100 m. Two layers with elevated phytoplankton concentrations are usually in evidence. The first of these occurs at a depth of 10–30 m and is associated with a photosynthesis-optimal light zone; the second lies at depths of 70–90 m and is related to heightened biogenic element levels in the vicinity of the pycnocline (Sorokin, 1976). As is evident from Table 1, the depth of the photosynthesis layer at all stations of both transects was usually slightly in excess of 100 m. As a rule, only a single photosynthesis peak was observed (the one in the 15–25-m depth range), since the pycnocline lay below the photosynthesis layer boundary (see Table 1). However, Stations 122 and 126 did exhibit a second relatively small primary production peak at 70 m (Table 1). Primary production values for the topmost levels of the water column were usually markedly lower than at depths of 10–15 m, which was probably due to photic inhibition of photosynthesis by the high-intensity incident light. Stratification of water masses over the water column had no significant effect on primary organic-matter production by phytoplankton, inasmuch as the top 100 m of the water column was homothermal. Thus, the water temperature in the top 100 m of the water column at stations of both transects varied within just 1–2°C. Salinity in the same layer varied within the same narrow limits, so that the primary production level at various depths depended largely upon light intensity, amount of phytoplankton present, and biogenic-element availability.

The local primary production peaks occurring at a depth of 70 m at Stations 122 and 126 were probably due to the elevated levels of biogenic elements present there.

The values obtained for primary production of organic matter by phytoplankton for the whole of the photosynthetic zone ranged from 70 to 140 mg C/m²/day (see Table 1). The maximum phytoplankton production (140 mg C/m²/day) was observed at Station 116; minimum production (70 mg C/m²/day) occurred at Station 120 (Table 1). The total average levels of phytoplankton productivity in this part of the Pacific during the period of our studies was in line with the higher range of primary phytoplankton production values typical of oligotrophic zones of the World Ocean (i.e., about 101 mg C/m²/day).

For stations of the second transect, situated to the northwest of the first at about 8°N, the range of variation of primary production rates (90–338 mg C/m²/day) exceeded the range of values for Stations 114–120 (Table 1). The mean primary production at Stations 121–126 corresponded to the lower range of productivity rates for oligomesotrophic zones of the World Ocean (i.e., about 172 mg C/m²/day) (Table 1).

Comparing the primary organic-matter production values measured during the 1988 expedition with those obtained

during the 1984 expedition, which covered roughly the same parts of the Pacific, we note that both primary productivity and the range of variation of primary production rates were greater in 1984. The rates of primary production of organic matter by phytoplankton over the Marianas transect in late July–early August 1984 ranged from 100 mg C/m²/day to 1.16 g C/m²/day, the mean value being about 400 mg C/m²/day. The highest primary production values for phytoplankton occurred at the westernmost stations of the transect. The rather high primary production rates in this part of the ocean in 1984 were probably due to the seasonal arrival of waters rich in biogenic elements that originated in the equatorial divergence area to the south of the study area.

Phytoplankton productivity rates for the Marianas transect in 1988 were somewhat lower than those recorded in 1984. The differences can probably be attributed to fluctuations in the arrival of waters from the equatorial divergence region. On the whole, the level of primary production of organic matter in the central tropical Pacific was in keeping with expectations based on previous studies (Sorokin, 1976) and on the findings of the 1984 expedition, corresponding more or less to the level associated with oligomesotrophic zones of the World Ocean.

TABLE 1
Primary production (mg C/m²/day) at different stations
in the central Pacific.

Depth (m)	114	115	116	119	Station Number		122	123	124	125	126
0.5	2.9	1.7	2.3	1.2	0.42	3.5	1.9	2.9	0.40	1.2	1.4
10	1.7	2.3	2.5	1.8	1.2	5.2	5.6	2.7	0.48	0.53	3.0
15	1.5	2.6	5.6	3.6	1.6	7.2	10.5	6.0	2.7	2.7	4.5
25	2.8	1.1	1.5	2.1	1.3	1.7	7.8	2.0	3.4	3.7	2.7
45	0.7	0.6	1.0	1.6	1.0	0.74	1.3	0.97	0.45	1.3	0.6
70	0.44	0.32	0.6	0.58	0.16	0.74	2.3	0.3	0.3	0.46	0.7
100	0.06	0.02	0.08	0.14	0.02	0.21	0.13	0.01	0.00	0.05	0.0
* P _{m2}	80.5	84.2	140	132	70	177	338	143	89	125	16?

* P_{m2} is the primary production for the photosynthesis layer down to 100 m (mg C/m²/day).

3.3 Mesozooplankton

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Materials and Methods

The materials for this work were collected in the eastern equatorial region of the Pacific Ocean at seven stations (Stations 114–120) whose coordinates ranged from 10°S to 150°W, and 0°S to 178°W (Fig. 1). The zooplankton was collected in daylight with a large Juday Net, with a mesh of 168 µm and a

throat diameter of 37 cm, from the 0–50, 50–100, and 100–200-m levels. The samples were fixed with a 40% solution of formaldehyde and were processed by the standard methods (Korshenko, 1988; Tsyban *et al.*, 1988) under an MBS-9 binocular microscope in a Bogorov chamber. The sample was concentrated and poured into a Petri dish. While it was being examined under the binocular microscope, the

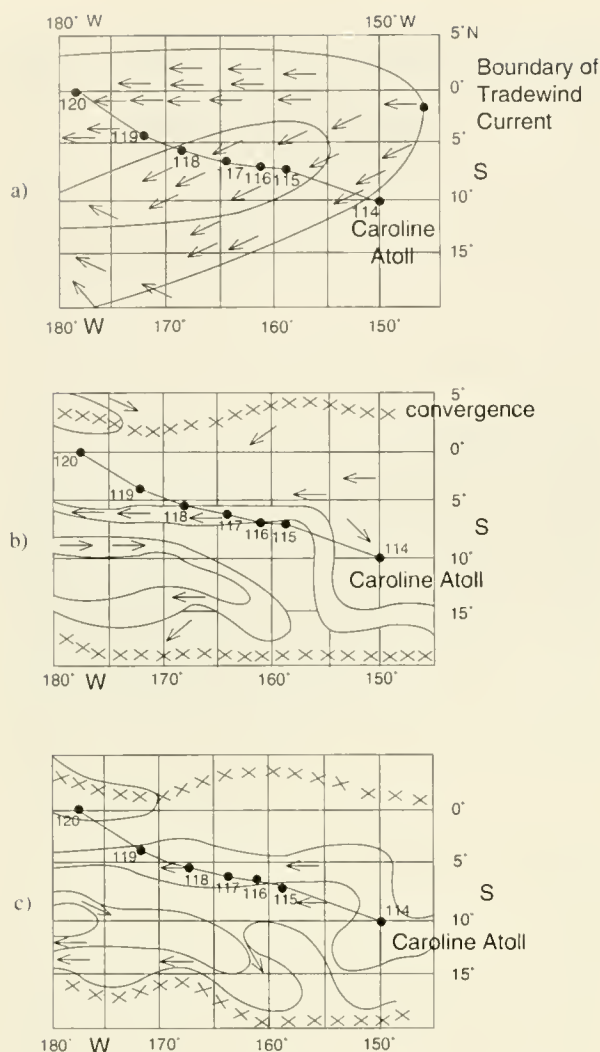


Fig. 1. Character of currents in the region studied: (a) circulation of waters at the surface; (b) circulation of waters at a depth of 100 m; and (c) circulation of waters at a depth of 200 m.

largest animals (over 2 mm long) were washed out and classified into systematic groups using a biolam R-7 microscope. The residue of the sample was diluted 10–20-fold, depending on the concentration, and 2–3 portions of 10–20 ml each were taken with a 5-ml plunger pipet for counting. On the basis of this data, the mesozooplankton numbers in 1 m³ and under 1 m² were calculated. A micrometer eyepiece was used to determine the body length of representatives of each species. On the basis of these values and Chislenko's nomograms (Chislenko, 1968; Vinogradov & Shushkina, 1987), the biomass of each species was determined, and the total biomass of mesozooplankton in 1 m³ and under 1 m² was calculated. Twenty samples were analyzed.

Results and Discussion

It is well known (Korshenko, 1988) that the characteristics of the distribution of zooplankton depend, to a considerable degree, on the hydrological structure of the water masses. Figure 1 shows a diagram of the currents in the studied region on the surface and at depths of 100 m and 200 m. The dynamics of the water masses at the easternmost station near Caroline

Atoll and at adjacent Station 114 are low; no major currents pass through this area. The depths of 100 m and 200 m at stations in the central portion of the region are characterized by a water mass transport to the west. The water masses of the western portion of the section (Stations 119 and 120) are affected by the surface South Tradewind Current. In addition, at the westernmost point of the region (Station 120), an anticyclonic equatorial current is observed (Gorshkov, 1974).

The heterogeneity of the regional water structures suggests a nonuniform horizontal and vertical distribution of the mesozooplankton as well as its qualitative diversity. As is evident from Table 1, the composition of the mesozooplankton differed qualitatively at different points of the section. A total of about 180 forms of mesozooplankton were determined as a result of the analysis of the samples. The average number of species for a station ranged from 75 to 139 and, for an individual level, from 39 to 84 (i.e., it differed by a factor of two) (Table 1; Fig. 2). The smallest number of species was found at the station near Caroline Atoll; at the 0–50-m and 50–100-m levels, there were 39 and 56 species, respectively. The number of species increased from south to north toward the equator, reaching a maximum of 139 at Station 17. The vertical structure of species composition also varied. In the majority of the cases, the number of species increased appreciably with depth, and it remained practically unchanged only at the equator (Fig. 2a).

The species observed in the waters of the region studied were encountered at different frequencies. Four gradations of species occurrence were distinguished: rare, under 1 sp/m³;

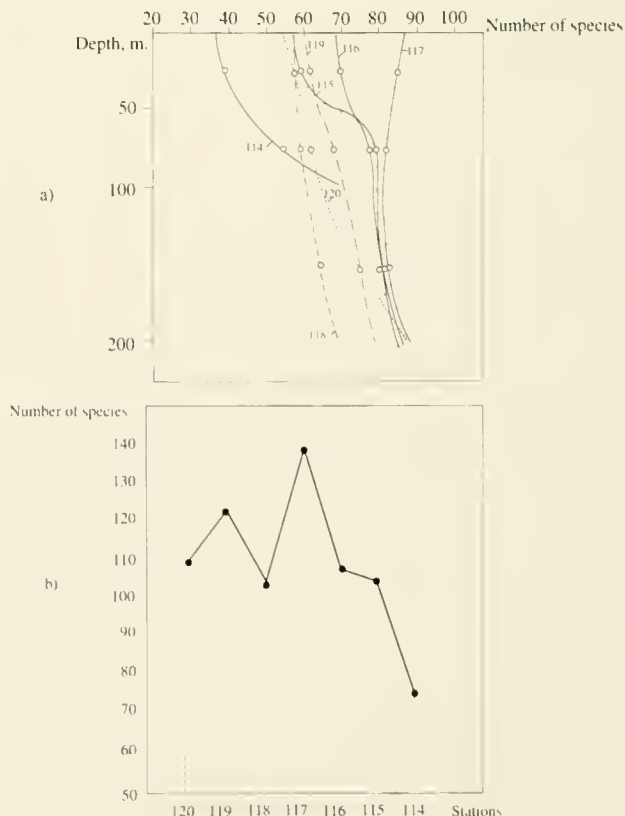


Fig. 2. Number of mesozooplankton species: (a) at an individual level; and (b) average for the station.

low, from 1 to 10 sp/m³; normal, from 10 to 100 sp/m³; and massive, > 100 sp/m³ (Table 1). As a rule, determined forms of mesozooplankton were found at the same frequency. However, it is evident from Table 1 that, in many cases, the frequency of species occurrence increased in the western portion of the section. The number of massive species at an individual level ranged from 4 to 14. The maximum number of massive species (13–14) was recorded in the western portion of the section at the equator; the minimum number was recorded in the eastern portion. We note that the populations of only 21 species of zooplankton reached numbers above 100 sp/m³; 18 consisted of the order Copepoda. Among other taxonomic groups, massive concentrations were formed by *Flissasagitta enflata*, *Oikopleura* sp. I, *Euphausia similis* var. "armata."

Some massive species reached a high density at all stations and levels. They included *Clausocalanus porgens*, *Oithona* spp., *Oncaea venusta*, *Corycaeus gibbulus*, *Microsetella rosea*, and *Oikopleura* sp. I. Of these, the most numerous species was the cyclopoid, *O. venusta*. On the other hand, 60 rare species occurring in 5–15% of the samples were counted. On the whole, the lists of planktonic organisms observed in equatorial waters of the Pacific Ocean (Geinrikh, 1960; Vinogradov & Voronina, 1963; Arashkevich, 1972; Stepan'yants, 1977) are similar to those that we obtained (Table 1).

Mesozooplankton species composition in the section from Caroline Atoll to the equator was approximately uniform, from east to west for species of Cyclopoida, Harpacticoida, Appendicularia, and Siphonophora, as well as for the minimal content of Euphausiacea and Chaetognatha (Fig. 3, Table 1). In the eastern portion of the region, such groups as Ostracoda, Mysidae, and Salpidae were practically absent. Of the 13 determined Polychaeta, only two species were detected in the region near Caroline Atoll. Some species of Chaetognatha (i.e., *Ferosagitta ferox*, *Pterosagitta draco*, *Parasagitta speticoela*, *Sagitta* sp., *Sagitta pulchra*) found in the western portion of the region were absent from Station 114. Although species composition at the eastern stations was poor, relative to those to the west, some species were found there that were not found at any of the other stations (i.e., the Far-neritic [Vinogradov & Voronina, 1963] copepod *Undinula vulgaris* and certain siphonophores).

In the western section of the region, the number of species of Cyclopoida, Harpacticoida, Euphausiacea, Amphipoda, Calanoida, and Chaetognatha increased significantly, sometimes severalfold, in comparison with the eastern section (Fig. 3). As one moved toward the equator, from Station 117, the number of previously undetected deep-sea species of Calanoida (*Neocalanus gracilis*, *N. robustus*, *Bradycalanus* sp., *Rhincalanus cornutus*, *Bradyidus armatus*, *Euchirella amoena*, *Pleuromamma abdominalis*, *P. gracilis*, *Haloptilis acutifrons*, *H. longicornis*, *Candacia longimana*, and *Labidocera detruncata*) increased in the samples. This may have been due to a more intense mixing of equatorial waters in the region of their increase or to more active vertical daily migrations of mesozooplankton (Vinogradov & Voronina, 1963). The western section was also much richer in the species composition of Cyclopoida: previously undetected species of

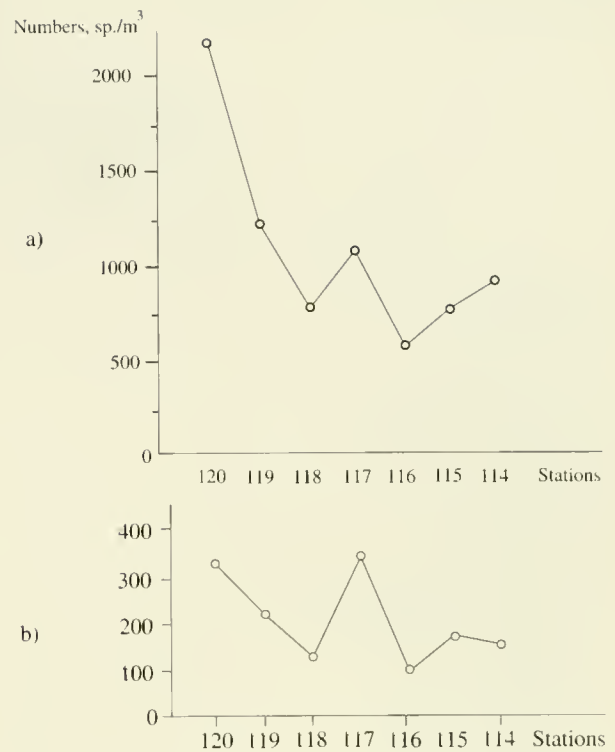


Fig. 3. Horizontal distribution of mesozooplankton in the 200 m surface layer: (a) distribution of numbers; and (b) distribution of biomass.

Corycaeus lautus, *C. robustus*, and six species of the genus *Sapphirina*, *Copilia longistylis*, and *Pachysoma dentatum* were present in the samples. The Harpacticoida group in the samples near Caroline Atoll was represented by the single species, *Microsetella rosea*. The new species of *Clytemnestra scutellata* and *Miracia* sp., from deeper waters, appeared in samples from the western stations. In contrast to the eastern section, where Amphipoda were represented by species in the family Hyperiididae, to the west, there were more species of Platyscelidae and Pronoidae. Isolated specimens of *Ramosia* sp., *Vogtia serrata*, and *Maresearsia sphaera*; representatives of the Gerionidae family; larvae of cephalopod mollusks; and large forms of Appendicularia (*Oikopleura* sp. II) were observed only in the western stations. Thus, moving from Caroline Atoll to the equator, the diversity and abundance of mesozooplankton increased.

Differences in species composition were characteristic not only of the extreme western and eastern points of the region: a number of interesting characteristics were also discovered at Station 117, located at the center of the region. All the taxonomic groups were represented most completely in the community of zooplankton found at this station. For example, of 30 species of Amphipoda, 22 were found at Station 117, and of 13 species of Polychaeta, 11 were found. Large forms of *Tomopteris* sp., *Oikopleura* sp. II, a single specimen of *Nematoscelis gracilis*, and concentrations of large *Euphausia similis* var. "armata" and tomopterids were also found in the waters of Station 117.

TABLE 1

Qualitative composition of mesozooplankton.
 (Notation: *-rare species, numbers below 1 sp/m³;
 **-low-number species, numbers from 1–10 sp/m³;
 ***-regular species, numbers from 10–100 sp/m³; and
 ****-massive species, numbers in excess of 100).

	114	115	116	117	118	119	120
1. Foraminifera	***	***	**	**	**	**	**
Radiolaria							
2. <i>Spongotrochus</i>		*	*				*
3. <i>Collosum</i> sp.		*	*	*		*	*
Hydrosia							
4. Gerionidae gen. sp.				*	*		
5. <i>Liriope tetraphylla</i>				*			
Siphonophora							
6. <i>Agalmia</i> sp.	*	*					
7. <i>Marrus</i> sp.			*				
8. <i>Ramosia</i> sp.						*	
9. <i>Vogtia serrata</i>			*			*	
10. <i>Maresearsia sphaera</i>						*	
11. <i>Sulculeolaria quadridentata</i>		*					
12. <i>S. quadrivalvis</i>				*		*	*
13. <i>Galettia australis</i>				*		*	
14. <i>Diphyes bojani</i>			*	*			*
15. <i>D. dispar</i>		*	*	*	*	*	*
16. <i>Lensia achilles baryi</i>	*			*			
17. <i>L. campanella</i>				*	*	*	*
18. <i>L. multicristata</i>		*					
19. <i>Lensia</i> spp.	*	*	*	*	*	*	*
20. <i>Muggiaea atlantica</i>	*						
21. <i>Eudoxoides mitra</i>		*	*	*	*	*	*
22. <i>E. spiralis</i>	*	*	*	**	**	**	**
23. <i>Chelphyes appendiculata</i>	*	*					
24. <i>C. contorta</i>	*	*	*	*	*	*	*
25. <i>Ceratocymba leucartii</i>	*		*	*			*
26. <i>Abylopsis eschscholtzii</i>	*	*	*	*	*		
27. <i>A. tatragona</i>		*		*		*	*
28. <i>Bassia bassensis</i>	*		*	*	*	*	
29. <i>Abyla schmidti</i>		*					
30. Diphyidae gen. sp.		*	*	**		*	
Polychaeta							
31. <i>Alciopa parasitica</i>		*	*	*		**	*
32. Alciopidae gen. sp.	*			**			
33. <i>Krohnia</i> sp.			*	*			
34. <i>Rhynchonerella</i> sp.		*		*		*	*
35. <i>Maupasia</i> sp.		*					
36. <i>Lopadorhynchus appendiculatus</i>	*	*	*	*	*		
37. <i>Pelagobia logicirrata</i>	*	*	**	*	**	**	
38. Phyllodocidae gen. sp.		*	*				
40. <i>Tomopteris elegans</i>		*	*	*	*	*	*
41. <i>Tomopteris</i> sp. II					*	*	*
42. <i>Travislopsis levinseni</i>		*	*	*	*	*	*
43. <i>T. lobifera</i>		*	*	*		*	*
44. Typhloscolecidae gen. sp.	*			*	*	*	*
Mollusca							
45. Cephalopoda larvae				*	*		
Crustacea							
46. Ostracoda: <i>Conchoecia</i> sp.		**	**	**	**	**	**
Copepoda							
47. <i>Calanus minor</i>	**	**	*	**	**	***	***
48. <i>C. pauper</i>		**	**	**	**	***	***
49. <i>Neocalanus gracilis</i>		*	*	*		*	
50. <i>N. robustior</i>		*	*	*	*	*	
51. <i>Neocalanus</i> spp. cop.		*	*	*	*		
52. <i>Undinula darwinii</i>	***	***	**	***	**	***	***
53. <i>U. vulgaris</i>	*	*					
54. <i>Calanus</i> spp. cop.	**	***	***	**	**	***	***
55. <i>Bradycalanus</i> sp.						*	*
56. <i>Eucalanus attenuatus</i>	**	**	**	**	**	**	**
57. <i>E. subcrassus</i>		*	*	**		**	*
58. <i>Rhincalanus cornutus</i>				*		*	*

TABLE 1 - continued

	114	115	116	117	118	119	120
59. <i>Acrocalanus gibber</i>	*	**	**	**	*	**	**
60. <i>A. gracilis</i>		***	**	***	**	***	***
61. <i>A. monachus</i>	**	**	**	**	**	**	**
62. <i>Calocalanus pavo</i>	**	***	**	***	*	***	**
63. <i>Paracalanus aculeatus</i>	***	***	***	***	***	***	***
64. <i>Mecynocera calusi</i>	***	**	***	***	***	***	***
65. <i>Clausocalanus arcuicornis</i>	***	**	*	***	***	*	***
66. <i>C. pergens</i>	****	****	****	****	****	****	****
67. <i>Pseudocalanus minutus</i>		*					
68. <i>Pseudocalanidae</i> gen. sp.	****	**	****	****	****	****	****
69. <i>Bradyidus armatus</i>				*			
70. <i>Euchirella amoena</i>					*	*	*
71. <i>Aetidae</i> gen. sp.							
72. <i>Enchaeta marina</i>	***	**	**	***	***	***	***
73. <i>Scolecitricella orientalis</i>			**	**	**	***	***
74. <i>Scoletrix danae</i>	**	**	**	**	**	**	**
75. <i>Phaena spinifera</i>		*	*		*		
76. <i>Centropages calaninus</i>		*	*	**	*	*	*
77. <i>C. elongatus</i>	*		*				
78. <i>C. gracilis</i>	*	*	*	*	*	*	*
79. <i>C. longicornis</i>		*	*	*	*	*	*
80. <i>Centropages</i> spp. cop.		**	*	*	**	**	**
81. <i>Pleuromamma abdominalis</i>				**		*	
82. <i>P. gracilis</i>			**	**	**		
83. <i>Lucicutia flavicornis</i>		*	*	**	**	**	**
84. <i>L. ovalis</i>		*	**	*	*	*	***
85. <i>Heterorhabdus papilliger</i>		*	*	**	*	*	**
86. <i>Haloptilis acutifrons</i>					*	*	
87. <i>H. longicornis</i>		*	*	*			*
88. <i>Candacia catula</i>	*	*	*	*	*	**	*
89. <i>C. longimana</i>				*			
90. <i>C. pachydactyla</i>	**	**	**	*	**	**	**
91. <i>C. truncata</i>	*	*	*	*	**	*	*
92. <i>Labidocera detruncata</i>							*
93. <i>Pontellina plumata</i>		*	*	*	*	*	*
94. <i>Arcatia negligens</i>	**	***	**	**	***	***	***
Cyclopoida							
95. <i>Oithona</i> spp.	***	***	**	***	**	***	***
96. <i>Oncaea venusta</i>	***	***	**	***	**	***	***
97. <i>O. notopus</i>				*			*
98. <i>Corycaeus agilis</i>					*	**	***
99. <i>C. asiaticus</i>	*						
100. <i>C. eatus</i>	**	**	*	**	*	**	**
101. <i>C. crassiusculus</i>	**	**	*	**	*	**	**
102. <i>C. flaccus</i>	**	***	*		**	*	*
103. <i>C. gibbulus</i>	***	***	***	**	**	***	***
104. <i>C. japonicus</i>		**	*	*			*
105. <i>C. laevis</i>						*	*
106. <i>C. longistylis</i>	**	*	*	**	*	*	*
107. <i>C. robustus</i>						*	*
108. <i>C. speciosus</i>		**	**	**	**	**	**
109. <i>Corycaeus</i> spp. cop.			**	**	**	**	**
110. <i>Sapphirina auronitens</i>				*	*	*	
111. <i>S. gastrica</i>				*	*		
112. <i>S. intestinata</i>					*		
113. <i>S. metallina</i>	*	*	*	*	*	*	
114. <i>S. nigromaculata</i>						*	*
115. <i>S. opalina</i>				*		*	*
116. <i>S. stellata</i>				*	*	*	*
117. <i>Sapphirina</i> spp. cop.				*	*		
118. <i>Copilia longistylis</i>							*
119. <i>C. mirabilis</i>	**	*	**	**	**	**	**
120. <i>C. quadreta</i>	*	*	*	*	*	**	*
121. <i>Pachysoma dentatum</i>			*			*	*
122. <i>Nogagus muraji</i>				*			*
Harpacticoida							
123. <i>Microsetella rosea</i>	**	**	**	**	**	***	**
124. <i>Clytemmestra scutellata</i>		*	*	*	*	**	**
125. <i>Miracia</i> sp.				*	*	*	*
126. <i>Copepoda nauplii</i>		**	**	**	**	**	**

TABLE 1 - *Continued*

	114	115	116	117	118	119	120
Mysidacea							
127. Mysidae gen. sp. larvae			**	*	*	**	
128. Gammaridae imm.							*
Amphipoda							
129. <i>Vibilia chuni</i>				*		*	*
130. <i>Paraphronima graciis</i>		*		*			
131. <i>Lestrigonus shizongeneias</i>	*		*	*	*	*	*
132. <i>L. shoemakeri</i>		*	*	*	*	*	*
133. <i>Hyperia fabrei</i>		*	*	*			
134. <i>Hyperietta stephensi</i>	*	*	*	*	*	*	*
135. <i>Phronima atlantica</i>				*			
136. <i>P. curvipes</i>			*		*		*
137. <i>Phronimella elongata</i>		*	*	**	*	*	*
138. <i>Phrosina semulmata</i>			*	*	*	*	
139. <i>Lycaeopsis zamboangae</i>				*	*	*	
140. <i>Eupronoe armatus</i>				*	*	*	*
141. <i>E. maculata</i>				*	*	*	*
142. <i>E. minuta</i>		*		*	*	*	
143. <i>Paralycaea gracilis</i>				*	*	*	
144. <i>Parapronoe parva</i>		*	*		*		
145. <i>Brachyscelus cruscum</i>				*			
146. <i>Oxycephalus longipes</i>	*	*					
147. <i>Leptocotis tenuirostris</i>				*			*
148. <i>Calamorrhynchus pellucidus</i>				*			
149. <i>Platyscelus armatus</i>	*			*			
150. <i>Pl. ovoides</i>			*		*	*	*
151. <i>Hemityphis tenuimanus</i>				*			
152. <i>Paratyphis parvus</i>		*					
153. <i>Paratyphis</i> sp.		*					
154. <i>Amphithyrus muratus</i>		**					
155. <i>Tetrathyrus forcipatus</i>				*			
Euphausiacea							
156. <i>Euphausia similis</i> var. <i>armata</i>				***		*	
157. <i>Euphausia</i> spp. <i>furcilia</i>	**	*		*	*	**	***
158. <i>Nematoscelis gracilis</i>				*			
159. <i>Stylocheiron affine</i>	*			*			
160. <i>Stylocheiron</i> spp. <i>furcilia</i>	*	*	*	*	*	*	*
161. <i>Euphausiacea caliptopici</i>		*	**	**	**	**	***
Decapoda							
162. <i>Decapoda</i> larvae	**	*	*	*	*	**	*
163. <i>Lucifer</i> sp.	*	*	**	**	*	*	*
164. <i>Echinodermata</i> larvae (<i>ophiopl.</i>)	*	**	*	**	**	**	**
Chaetognatha							
165. <i>Pterosagitta draco</i>		**	**	*	*	*	*
166. <i>Aidanosagitta</i> sp.	*	*	*	*			
167. <i>Ferosagitta ferox</i>		*		*	*	*	*
168. <i>E. robusta</i>	*	*		*	*	*	*
169. <i>Flassisagitta enflata</i>	**	**	**	**	**	***	***
170. <i>Parasigitta septicoela</i>						*	
171. <i>Sagitta pulchra</i>	*		*	*		*	
172. <i>Sagitta</i> sp.						*	
173. <i>Serratosagitta pacifica</i>	*	***	*	**	**	**	**
174. <i>Chaetognatha</i> spp. imm.	**	**	**	**	**	**	**
Thaliacea							
175. <i>Heliosalpa virgula</i>			*				
176. <i>Salpa</i> sp.		*	*	*			
177. <i>Iasis zonaria</i>		*					
178. <i>Weelia cylindrica</i>			*				
179. <i>Salpidae</i> gen. sp.		*	*	*	*	*	*
Doliolidae							
180. <i>Thalia democratica</i>	*			*		*	
181. <i>Dolioloides rarum</i>	*	*	*				
182. <i>Doliolidae</i> gen. sp.	**	*	*			*	*
Appendicularia							
183. <i>Oikopleura</i> sp. I	***	***	***	****	***	****	****
184. <i>Oikopleura</i> sp. II				*			*
185. <i>Pisces</i> larvae		*	*	*	*	*	*

As noted previously, the distribution of mesozooplankton within the region is mainly due to the heterogeneity of hydrological conditions found there (Korshenko, 1988). As a result, two bands of increased zooplankton biomass are formed in the surface layer along the equator (Vinogradov & Voronina, 1963). In the Southern Hemisphere west of 140°W, the zone of abundant plankton narrows to 5°S–4°S. At the same time, zooplankton productivity in the equatorial region increases from east to west. We found that zooplankton biomass ranged from 51 to 200 mg/m³. The western portion of the region (Stations 119 and 120) was located in the zone of abundant plankton (Fig. 1). The total biomass of mesozooplankton ranged from 89 to 340 mg/m³ and averaged 201 mg/m³ (Table 2). The total biomass of zooplankton in the eastern portion of the section in the upper 200 m layer did not exceed 163 mg/m³ (Fig. 3). At the westernmost point, and at Station 117, the biomass was maximum and amounted to 321 and 340 mg/m³, respectively. The total numbers of mesozooplankton at different stations ranged from 547 to 2,170 sp/m³ and averaged 1,044 sp/m³ (Fig. 3; Table 2), which doubled the known quantity of plankton organisms (493 sp/m³) known in the northern portion of the equatorial region (Korshenko, 1988). In the eastern section, the numbers of mesozooplankton ranged from 547 to 765 sp/m³. As one moved toward the equator, starting at 6°S, the numbers of mesozooplankton increased to a maximum of 2,170 sp/m³ at Station 120 (Table 2). It was shown that the qualitative composition and structure of the community at Stations 117 and 120 differed appreciably from those recorded at the other stations in the region. This is evidently related to the characteristics of the structure and dynamics of the water masses.

The vertical distribution of the mesozooplankton was also different at different stations. At six of seven stations (Fig. 4), most of the mesozooplankton was concentrated in the upper 100-m layer, and the maximum was in the 0–50-m layer (Table 3; Fig. 4), corresponding to findings cited by Korshenko (1988). A significant increase in zooplankton numbers and biomass with depth was tracked only at the westernmost point (Station 120). Mesozooplankton biomass as a whole increased with depth owing to an increase in the fraction of large-sized animals.

In addition to analyzing the vertical distribution of total numbers and biomass, we also examined the vertical distribution of individual taxonomic groups. We found that the numbers of Calanoida and Euphausiacea decreased with depth, yet the biomass remained practically unchanged because of an increase in the fraction of large-sized forms (Fig. 5; Table 3). The numbers and biomass of Siphonophora, Polychaeta, Ostracoda, Haptracticoida, Amphipoda, Chaetognatha, and Salpidae increased with depth. The numbers and biomass of Cyclopoida, Mysidae, Decapoda, and Echinodermata, on the other hand, decreased with depth. The numbers of Doliolidae were constant at all the levels, and the biomass increased with the relative content of large-sized animals.

In order to analyze the structure of the mesozooplankton community, we divided the determined forms into 17 major systematic groups. The frequency of occurrence (by numbers and biomass) of 14 of these basic taxonomic groups is shown in Table 4. The maximum fraction of numbers, as an average for the cross section, belonged to Calanoida—53.8%. In 60% of the cases, Calanoida comprised over half of the total numbers. According to Korshenko (1988), the numbers of Calanoida in the 0–200-m layer amounted to 45% of the total value. The highest numerical percentage of Calanoida (66.5%) was found on Station 114. In the western portion of the section, Calanoida numbers decreased to 40%. The biomass amounted to over half of the total value only in the region of the Caroline Atoll, owing to the small number of other taxonomic groups composing the community. To the west, the relative content of Doliolidae was comparatively high, and the fraction of groups other than Calanoida was insignificant. We noted a tendency for the number of taxonomic groups to increase toward the equator. On one hand, the fraction of numbers and biomass of the dominant group (Calanoida) decreased, while the relative content of Cyclopoida, Chaetognatha, and Siphonophora increased. For example, the fraction of numbers and biomass of Cyclopoida at the equator was 48 and 29%, respectively. In addition to the general tendency of the Calanoida fraction to decrease, in many cases the typical (Fig. 6) structure of the community broke down as a result of concentrations of animals of a particular species. For example, the biomass fraction of Euphausiacea was maximum (35.5%) at Station 117 as a result

TABLE 2

Total numbers and biomass of mesozooplankton in the 200 m surface layer.

Stations	Numbers, sp/m ³				Biomass, sp/m ³			
	0-50	50-100	100-200	0-200	0-50	50-100	100-200	0-200
114	755	775	-	765	158	131	-	144
115	1,354	826	428	759	148	202	150	163
116	791	806	246	547	87	158	55	89
117	2,056	1,153	523	1,063	387	290	342	340
118	1,028	704	699	783	124	122	146	134
119	1,170	1,947	878	1,218	227	220	211	217
120	1,439	2,137	2,560	2,170	126	226	466	321
Average values	1,127	1,193	889	1,044	180	193	228	201

Remark: For Station 114, the data and results were obtained for the 0-100 m layer.

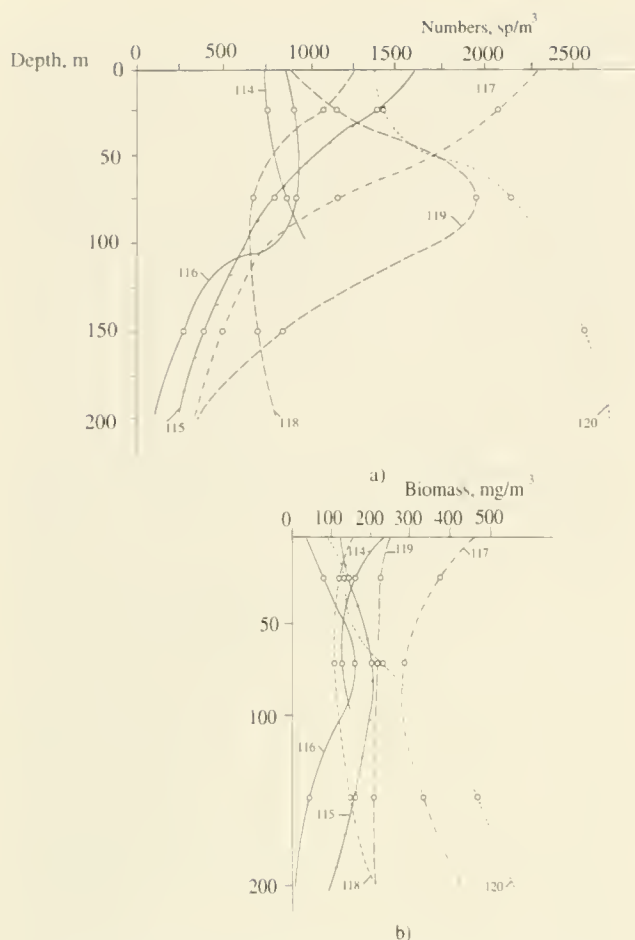


Fig. 4. Vertical distribution of mesozooplankton; (a) vertical distribution of numbers; and (b) vertical distribution of biomass.

of massive development of *Euphausia similis* var. "armata" in this area. Korshenko (1988) noted a similar case for a population of *E. similis*. The same value (35.5% of total biomass) was shown by the biomass fraction of Chaetognatha at specific levels of the western portion of the section. A typical portrait of the structure of the mesozooplankton community of the region is shown in Fig. 6.

The general pattern of variability of the vertical structure had the following characteristics: both the numbers and biomass of Calanoida, Decapoda, and Appendicularia and the biomass fraction of Cyclopoida and Siphonophora decreased with depth. The relative content of other groups (Harpacticoida, Amphipoda, Euphausiasea, Ostracoda, Chaetognatha, Salpidae, Doliolidae, Siphonophora, and Polychaeta) increased with depth.

Conclusion

1. The qualitative composition of the mesozooplankton was nonuniform in the region studied. As one moved toward the equator, species diversity of the zooplankton increased. The smallest number of species was recorded in the region of Caroline Atoll. In the majority of cases, the number of species increased with depth. It was postulated that the heterogeneity of the horizontal and vertical distributions of mesozooplankton resulted from vertical daily migrations and equatorial ascents of the water masses.

Twenty-one species of mesozooplankton reached numbers above 100 sp/m³; of these groups, the group of the most diverse composition was Calanoida. The number of massive species increased from east to west.

TABLE 3

Vertical distribution of mesozooplankton.

Levels Taxons	0 - 50 m		50 - 100 m		100 - 200 m	
	N	B	N	B	N	B
1. Siphonophora	3.2	17.2	5.3	19.4	7.7	20.5
2. Polychaeta	2.1	3.2	2.6	3.3	3.8	6.2
3. Ostracoda	0.3	0.2	1.2	1.0	4.4	3.5
4. Calanoida	687.0	60.9	588.0	65.6	424.0	59.0
5. Cyclopoida	553.0	30.0	429.0	38.1	328.0	23.0
6. Harpacticoida	31.0	0.2	73.0	0.5	47.0	0.6
7. Amphipoda	1.3	5.2	2.6	9.8	3.6	9.8
8. Mysidae	1.2	0.1	2.6	0.3	0.7	0.1
9. Euphausiasea	12.7	19.7	3.4	18.3	13.3	21.8
10. Decapoda	1.7	3.0	1.6	2.2	1.1	1.8
11. Echinodermata	5.9	0.0	4.7	0.0	3.2	0.0
12. Chaetognatha	13.5	21.4	17.8	24.7	25.3	57.6
13. Salpidae	0.8	10.4	1.5	3.1	1.6	14.2
14. Doliolidae	0.9	14.4	1.4	20.4	1.0	18.3
15. Appendicularia	154.0	4.9	69.1	2.1	33.7	1.0
16. Pisces	0.6	2.1	1.3	3.6	0.8	2.3
All Groups	1,227	180	1,193	193	889	228

N - average numbers, sp/m³

B - average values of biomass, sp/m³

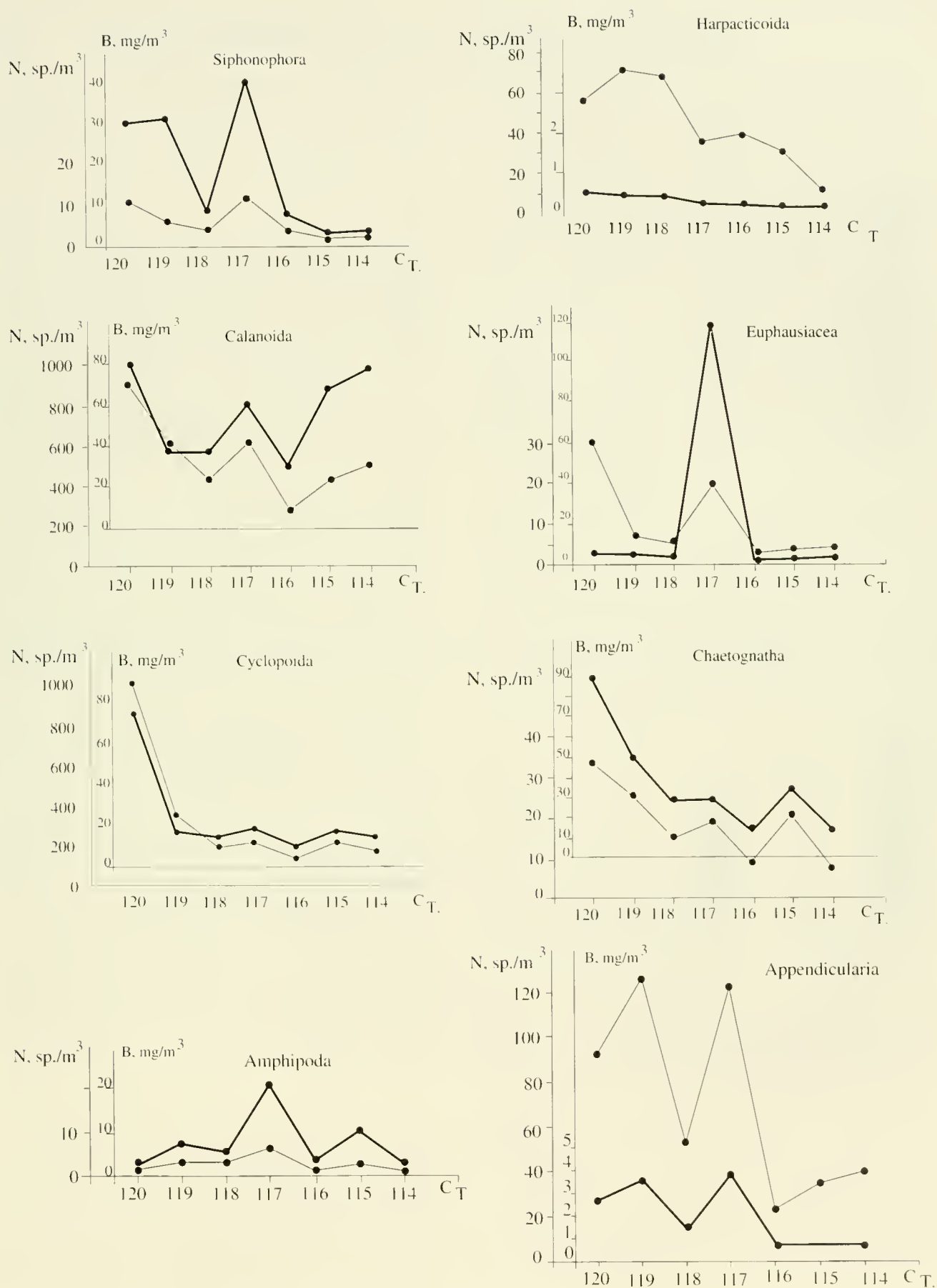


Fig. 5. Horizontal distribution of the main taxonomic groups of mesozooplankton.

TABLE 4

Structure of mesozooplankton community.

Stations	114		115		116		117		118		119		120		Average values	
Taxa	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B	% N	% B
1. Syphonophora	0.3	2.5	0.1	1.3	0.3	7.8	1.4	10.5	0.6	7.1	0.5	17.8	0.4	8.4	0.5	7.9
2. Polychaeta	0.0	0.0	0.3	2.5	0.4	2.2	0.5	2.3	1.3	0.3	0.4	3.8	0.1	1.5	0.6	1.8
3. Ostracoda	—	—	0.3	0.8	0.4	1.8	0.3	0.4	0.9	1.1	0.2	0.8	0.1	0.3	0.3	0.7
4. Calanoida	66.5	54.3	55.9	42.8	51.0	34.0	57.9	20.1	56.2	31.9	48.8	34.8	40.0	28.2	53.8	33.7
5. Cyclopoida	24.8	10.2	30.2	11.3	28.2	12.2	20.6	4.5	24.2	10.5	30.0	9.6	47.9	28.9	29.4	12.4
6. Harpacticoida	1.4	0.0	4.2	0.1	6.6	0.2	4.3	0.2	8.4	0.2	5.1	0.2	2.6	0.2	4.7	0.2
7. Mysidae	—	—	—	—	0.2	0.2	0.0	0.0	0.1	0.1	0.2	0.1	—	—	0.1	0.1
8. Amphipoda	0.2	2.0	0.5	6.1	0.2	4.2	0.7	6.4	0.3	5.4	0.2	2.6	0.1	0.8	0.3	3.9
9. Euphausiacea	0.5	0.4	0.4	0.8	1.0	1.0	2.2	35.2	0.6	1.0	0.8	2.2	1.4	3.7	1.0	6.3
10. Decapoda	0.3	0.6	0.1	0.9	0.6	3.2	0.3	1.3	0.1	2.0	0.5	0.3	0.1	0.4	0.4	1.2
11. Chaetognatha	1.0	9.3	3.1	20.5	1.8	13.7	2.2	8.7	1.9	18.6	2.1	19.6	1.2	16.7	1.9	15.3
12. Salpidae	0.0	1.0	0.0	8.2	0.3	7.7	0.1	1.2	—	—	0.3	4.6	0.1	2.5	0.1	3.6
13. Doliolidae	0.2	18.3	0.1	3.6	0.1	10.4	0.1	3.3	0.1	11.3	0.1	1.5	0.0	6.0	0.1	7.7
14. Appendicularia	5.3	0.8	4.1	0.9	3.9	0.7	8.4	1.5	6.7	1.3	10.9	1.9	5.7	1.7	6.4	1.3

% N - fraction of total numbers

% B - fraction of total biomass.

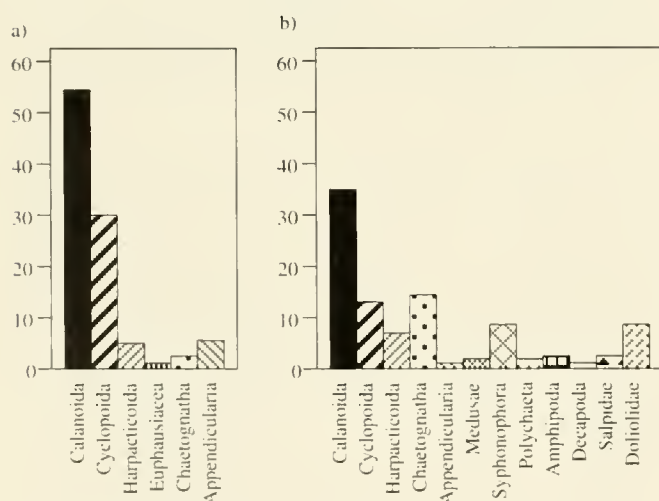


Fig. 6 Typical structure of mesozooplankton community: (a) structure of total numbers; and (b) structure of total biomass.

2. In numbers and biomass of mesozooplankton, this region can be characterized as medium-productive, with the western section more productive than the east. The station poorest in mesozooplankton was near Caroline Atoll. The average numbers of mesozooplankton were maximum in the 0–50-m layer and decreased with depth. On the other hand, the average biomass increased with depth owing to the increase in the fraction of large-sized forms.

3. The structure of the mesozooplankton community as a whole was characterized by the dominance of the fraction of numbers and biomass of Calanoida and Cyclopoida. In the majority of cases, half of the total consisted of Calanoida. In the western portion of the section, the relative content of other groups (Chaetognatha, Euphausiacea) increased, while the fraction of Calanoida decreased.

3.4 Zooneuston of the Tropical Pacific

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Introduction

Seventy-nine zooneuston samples were taken at 23 stations in tropical areas of the Pacific Ocean (Table 1). The sampling equipment consisted of a PNS-2 two-tier plankton-neuston net and an MNT fry-neuston trawl (Zaitsev, 1971). The PNS-2 net (mouth area 0.1 m²; mesh size 150 µm) permitted simultaneous manual skimming of the upper surface of the upper layers of the pelagial (i.e., of neustal [0–5 cm] and subneustal [5–25 cm]). The MNT trawl (mouth area 0.39 m²; mesh size 350 µm) made possible high-speed catching of mobile neustons at a vessel trawling speed of 3 m/s. The average skim duration was 10 min.

To facilitate the study of neuston community formation, the whole of the ocean area investigated was subdivided into three types of zones, namely 1. atoll lagoons (shallow water; complete or partial isolation from the ocean; developed littoral communities); 2. semienclosed marginal seas (relatively little exchange with the ocean; mostly shallow water; well-developed pelagic-shelf communities); and 3. open-ocean waters (pelagic communities predominant). The sampling effort covered an extensive portion of the tropical Pacific from Caroline Atoll in the east (154°51'E). The latitudinal limits of station locations were 11°20'N and 8°40'S.

TABLE 1

Neuston sample collection in the tropical Pacific.

Area	Number of		
	Stations	Samples	
		PNS-2	MNT
Caroline Atoll	3	22	--
Caroline Atoll/Phoenix Islands	4	8	4
Phoenix Islands/Gilbert Islands	6	12	1
Marianas sector	5	10	4
South China Sea	5	18	--
Total	23	70	9

The neuston (surface plankton) of the tropical Pacific has been described in publications of a general character (Geinrikh, 1964). There are also papers on the distribution of its individual components (e.g., of copepods of the Pontellidae family [Sherman, 1963; Voronina, 1964] and oceanic water striders of the genus *Halobates* [Herring, 1961]). Results of pleuston studies are reported in a major survey paper by Savilov (1969).

The need for the present study was dictated by a considerable hiatus in observations, as well as by the scarcity of quantitative data on neuston distribution in conditions of increasingly widespread and intense pollution of the World Ocean.

The zooneuston of the tropical Pacific found during the present studies was represented by epineuston consisting of oceanic water striders (*Halobates*) as well as by hyponeuston: copepods of the family Pontellidae, marine snails of the genus *Janthina*, larvae of benthic invertebrates, and fishes. In addition, allowance was made for the usual neuston components in the form of semisubmerged organisms: *Physalia* (Siphonophora), *Velella velella*, and *Porpita pacifica* (Chondrophora).

Analysis of the quantitative distribution of organisms leads to some basic conclusions regarding the distinctive features of neuston in the types of water areas studied.

The average counts of animals in the open ocean and in the South China Sea were comparable (2,730 and 3,160 ind/m³), while the concentration of animals in the lagoon at Caroline Atoll was 50 times lower. Larger organisms (medusae, salps, fish larvae and fry, euphausiids hyperiidea, et cetera) constituted a considerable fraction of the total neuston biomass, accounting for as much as 2.5 g/m³ (Station 119) and sometimes attaining values an entire order of magnitude higher (Station 128), where *Porpita* were dominant.

The relative neuston content was richer in Caroline Atoll's lagoon, the reverse of that for animals overall (Table 2). The low numbers of oceanic animal species in the lagoon against a background of early developmental stages of benthic invertebrates (Decapoda, Gastropoda, Cirripedia, et cetera) were due to shallowness of the waters and their relative isolation from the open ocean. The distinctiveness of the individual sea area categories (atoll, marginal sea, open ocean) was clearly evident from the proportion of benthic animal larvae in the total neuston count. Their percentage content decreased steadily from its maximum value of 99% in the lagoon to 75% in the South China Sea and 46% in the open ocean. The epineustonic *Halobates*, which breed along coasts, were similarly distributed, while the Pontellidae distribution behaved inversely (0.24% and 54%, respectively).

In addition to benthic-invertebrate larvae, the neustal also contained large numbers of pelagic animals at early stages of ontogenesis, which validates calling neuston "the ocean's breeding ground."

Comparison of the numbers of organisms in the microlayers investigated confirmed the existence of conditions conducive to neuston growth in all of the water areas studied. The sole exception to this rule was the waters of the Marianas sector (Stations 121–126) (Table 3).

TABLE 2

Components (counts expressed as individuals/m³) of neuston biocoenoses in the basic water area types of the tropical Pacific.

Component	Basic water area type		
	Caroline Atoll lagoon	South China Sea	Open waters of the Pacific
1. Pleuston	0	1.27	0.20
2. Epineuston	0.31	0.13	0.05
3. Hyponeuston	37.36	188.35	164.13
a) benthic-invertebrate and fish larvae	37.36	143.15	75.71
b) Pontellidae and <i>Janthia</i>	0	45.20	88.42
4. Others*	26.63	2,968.9	2,566.6
Relative neuston content, %	59	6	6

* This category groups together mesozooplankton components found in the surface layer, but distinct from the enumerated categories of organisms in being more uniformly distributed over the water column.

TABLE 3

Dominance of organisms in neustal expressed as a percentage.

Sea area	%
Caroline Atoll lagoon	1.3 ± 0.1
South China Sea	2.5 ± 0.6
Open ocean	1.5 ± 0.3
Marianas sector	0.9 ± 0.4

A degree of symmetry of neuston distribution with respect to the equator was noted (see Fig. 1). This was evidence of the effect of the northern and southern tradewind currents and of the anticyclonic current between them.

The observed pattern of organism distribution agrees with the data of Voronina (1964), who established that peak counts of the most common pontellid *Pontella tenuiremis* occurred at 1°N and 1°S. The meridional components of surface current

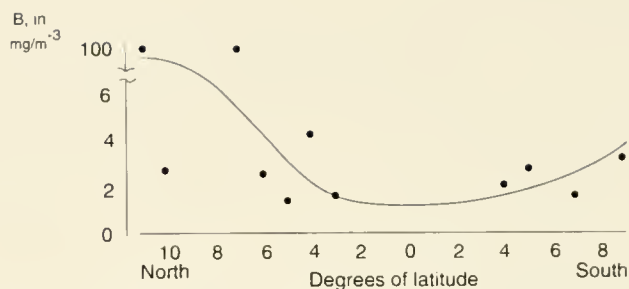


Fig. 1. Latitudinal distribution of neuston biomass (B) in the tropical waters of the Pacific Ocean.

point outwards from the equator, so that species that inhabit the topmost water layer are constantly carried away from it. The departing water is replaced by deeper-lying water free of surface animals. The result is an acute trough in surface species along the equator (Sverdrup *et al.*, cited by Voronina, 1964).

Constituting an agglomeration of hydrobionts, neuston attracts both aquatic and aerial predators. We know, for example, that decapod crustacean and pontellid larvae are part of the diet of tunas, bonitos, and other epipelagic fishes (Marchal, 1959). *Porpita* are consumed by marine turtles, while fish larvae and fry are food for marine snakes (Zaitsev, 1971). Neuston animals are an important part of the diet of seabirds. Flying fish are caught on the fly by frigate birds (Fregatidae) and terns (Laridae). Procellariiformes birds (*Puffinus*) have a variety of ways of feeding on neuston; albatrosses (*Diomedea*) and fulmars (*Fulmarus*) snatch their prey from the surface, and fork-tailed storm-petrels (*Oceanodroma*) do so while performing a "mincing walk" on water (Boaden & Seed, 1985). In waters close to shore, neuston is eaten by skimmers (Rhynchopidae) with their long cultiform gonyes (Zaitsev, 1971). According to the latest count (Day *et al.*, 1984), there are at least 50 species of birds that feed on neuston.

In conformity with what is usually the case with distribution in the ocean, neuston is most profuse in areas where currents converge. However, recent decades have seen a proliferation in the same areas of various kinds of plastic debris (Day *et al.*, 1984). Looking for neuston, marine birds often swallow these foreign objects, whose effect is invariably harmful and often fatal. With their high adsorption coefficients, oil lumps and plastic objects tend to have a buildup of toxic substances on their surface (Osipov & Charykov, 1987), thus inhibiting the development of invertebrates and fishes in the neustal. This, in turn, can only have a negative impact on the bioproductivity of the entire ocean.

3.5 Observations of Seabirds along a 14,892-km Cruise Track in the Tropical Pacific Ocean and the Bohol, Sulu, and South China Seas

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Introduction

This study forms a small part of the research efforts of the First Joint US–USSR Central Pacific Expedition (Line and Phoenix Groups, Gilbert Islands, Micronesia, inland Philippine Seas, and South China Sea). Seabird observations were made from the Soviet research vessel (R/V) *Akademik Korolev* (7,000 tons, 124 m in length) from Hilo, Hawaii, to Singapore (Figs. 1,2) via Christmas Island (02°N, 157°W) and Caroline Atoll (10°S, 150°W).

The primary objectives of the expedition were to characterize and contrast the fundamental oceanographic, hydrochemical, microbiological, hydrobiological, and ecological parameters of arctic and tropical marine ecosystems. Emphasis was placed on the primary productivity and ecological health of these two major areas, including pollution studies involving multidisciplinary experiments conducted jointly by scientists of both countries.

In this paper, we report the marine distribution of seabirds and other transoceanic migrants, such as shorebirds and ducks, during the tropical portion of the cruise, which covered 14,892 km from 9 September to 31 October 1988. We conducted a total of 161 hours of observations on transects representing an area of 3,609 km², during which time the ship traveled 4,511 km (Table 1). Our observations covered 21 degrees of latitude and 107 degrees of longitude. Because the cruise track traversed many island archipelagos, we subdivided it into the following 7 regions (Figs. 1,2), all lying between 14°N and 10°S latitudes:

Region I Line Islands, including waters south of Hawaii (150°W to 160°W);

Region II Phoenix Islands to the international dateline (160°W to 180°);

Region III Gilbert Islands (180° to 165°E);

Region IV Caroline Islands¹, Micronesia (165°E to 136°E);

Region V Philippine Sea and Basin (136°E to 125°E);

Region VI Inland Philippine Seas: Bohol (Mindanao) and Sulu Seas, Balabac Strait (125°E to 117°E); and

Region VII South China Sea, Philippines to Singapore (117°E to 103°E).

We interpret our results within the contexts of 1. breeding phenology, nonbreeding dispersion, and migration (Fig. 3); 2. proximity to known breeding colonies and nearest landfalls; 3. previous at-sea records; 4. anthropogenic factors such as population density, environmental alterations to coastal habitats, and pollution (see Chapters 2,3); and 5. general areas of upwelling, providing locally rich feeding areas.

Seabirds, more than any other group of living organisms, illustrate that the world's oceans are united. For example, parasitic jaegers (*Stercorarius parasiticus*) breed in Siberia and Alaska, then migrate south to winter in south temperate waters of the Pacific, Indian, and Atlantic Oceans. *En route*, in the Pacific, they skirt all four continents, passing through 150 degrees of latitude and at least 80 degrees of longitude.

The 1988 US–USSR expedition provided an opportunity to study assemblages of birds, highly visible indicators of the health of marine ecosystems, over vast areas of the Pacific Ocean. Studies of the marine environments utilized by these birds provide the knowledge to encourage practical action toward their conservation.

Previous Studies

Although the broad distributions of central and western Pacific seabirds are well-known (Murphy, 1936; Mayr, 1945; Delacour & Mayr, 1946; Baker, 1951; Clapp, 1967; Clapp & Sibley, 1967, 1968; Amerson, 1969; King, 1970, 1973, 1974a; Nelson, 1975, 1978; Perry, 1980; Engbring, 1983; Garnett, 1983, 1984; Gould, 1983; Harrison, 1985; Pratt, Bruner & Berrett, 1987), much remains to be learned of their detailed distribution patterns in the Southern Line Islands and areas west of Micronesia. Information on seabirds in southeast Asia, at least in English, is incomplete and often outdated (Delacour & Mayr, 1946; Delacour, 1947; King & Dickinson, 1975; Nelson, 1978; Harrison, 1985). We are unfamiliar with the literature in Asian languages and have not pursued the numerous reports and publications resulting from marine oriented trips to islands and reefs in the Asian region through which we passed (UNEP, 1984a,b; IUCN, 1988a,b), some of which may contain

¹ Not to be confused with Caroline Atoll (Island), Southern Line Islands, at 10°00'S latitude, 150°13'W longitude.

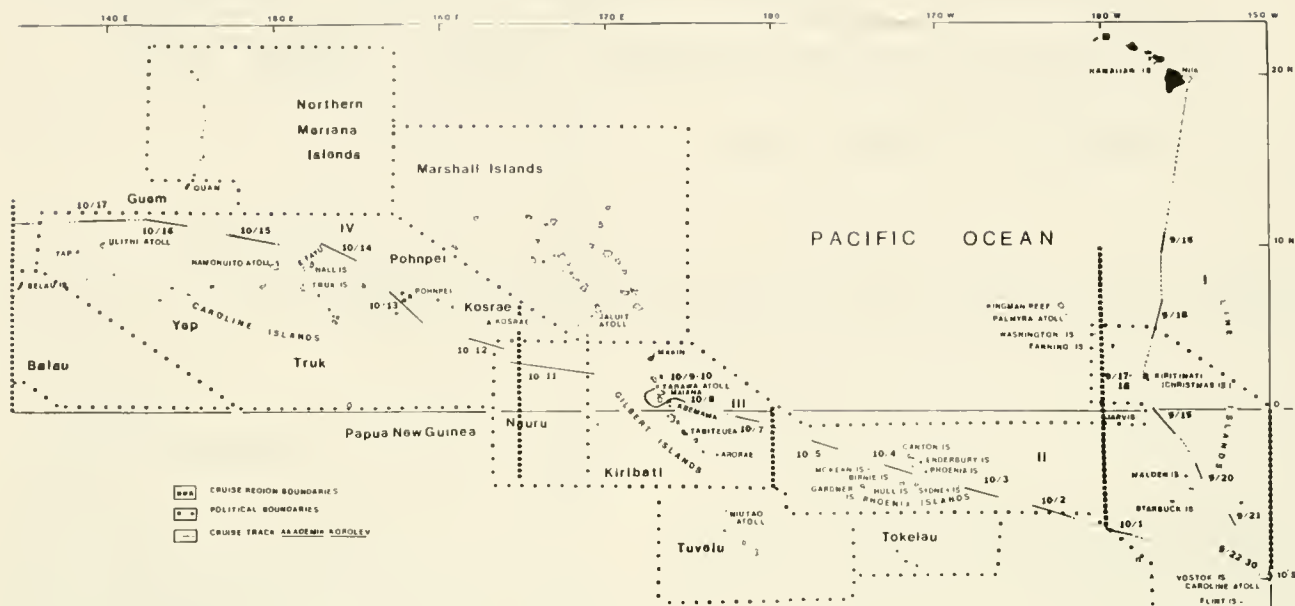


Fig. 1. Cruise track of the R/V *Akademik Korolev*: Regions I (Line Islands), II (Phoenix Islands), III (Gilbert Islands), and IV (Caroline Islands, Micronesia), 15 September–17 October 1988. Solid lines on cruise track represent daily observation hours, dotted lines, hours of darkness.

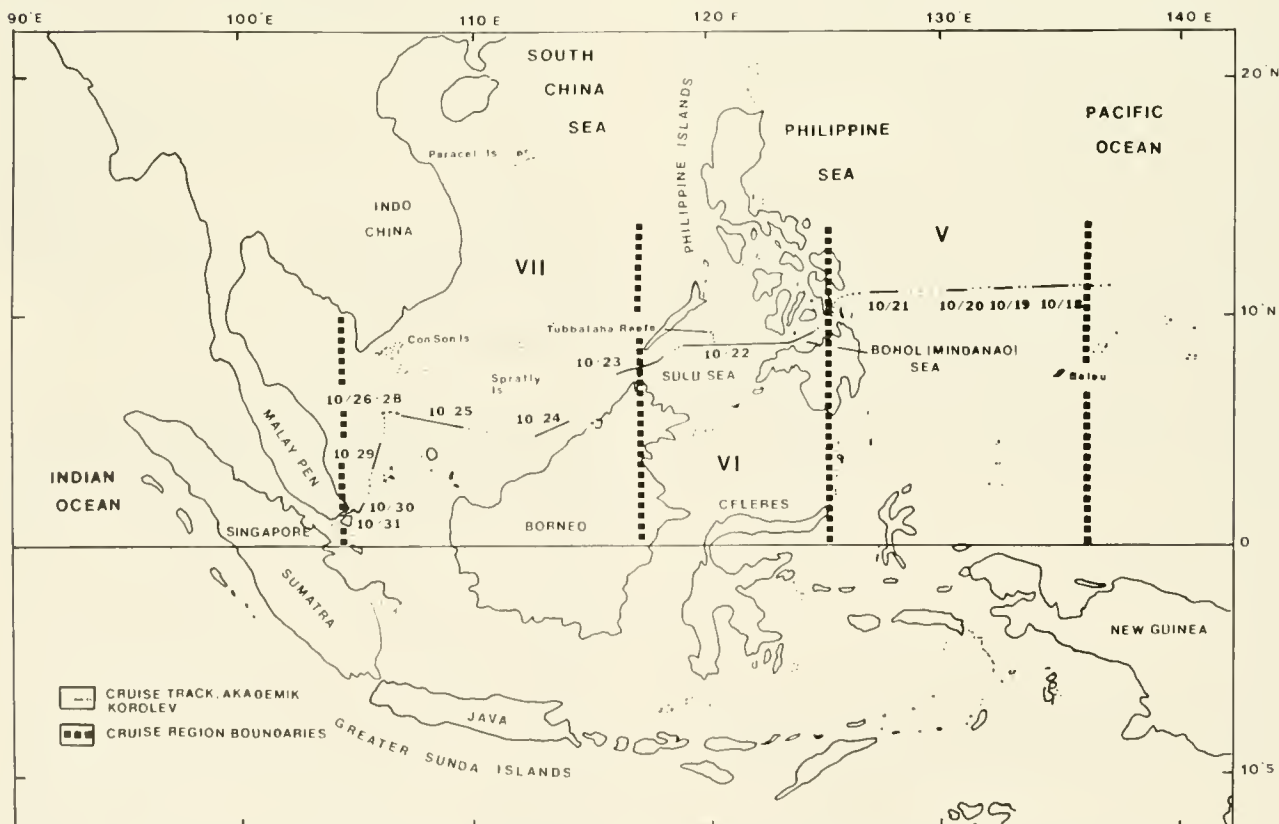


Fig. 2. Cruise track of the R/V *Akademik Korolev*: Regions V (Philippine Sea and Basin), VI (Bohol and Sulu Seas), and VII (South China Sea), 18–31 October 1988. Solid lines on cruise track represent daily observation hours, dotted lines, hours of darkness.

TABLE 1

Relative abundance of seabirds in each sector of the R/V *Akademik Korolev* cruise track, 15 September–31 October 1988.

	I	II	III	IV	Region V	VI	VII	Total
Observation Hours ¹	29.95	21.88	18.00	42.78	13.70	14.57	20.45	161.33
Kilometers Traveled During Observations	772.91	656.73	554.70	1,210.87	356.67	404.14	555.38	4,511.41
Area Covered by Observations (km ²)	618.33	525.38	443.76	968.70	285.34	323.31	444.31	3,609.13
No. Bird Species Seen	27	25	14	19	6	4	8	46
No. Individuals Seen	457	1,796	495	799	34	22	65	3,668
Average No. Birds Seen/hr	15.3	82.1	27.5	18.7	2.5	1.4	3.2	22.7
Average No. Birds Seen/10 km of Observations	5.9	27.3	8.9	6.6	1.0	0.5	1.2	8.1
Average Bird Density Per 10 km ²	10.20	45.72	14.6	10.38	1.76	1.63	3.95	12.61
No. Families Seen	7	7	5	9	4	4	4	11

¹ Each hour is the combined total of two people simultaneously viewing opposite sides of the ship, and thus equals 2 hours of observation in some other papers.

relevant seabird records. Most of the previous information on breeding and at-sea distribution of tropical seabirds was gathered from 1963 to 1969 (Humphrey, 1965) by the US National Museum's (Smithsonian Institution) Pacific Ocean Biological Survey Program (POBSP).

Methods

Daily at-sea observations were conducted from the flying bridge of the R/V *Akademik Korolev*, 12 m above the sea surface and within a viewing arc of approximately 180°. During the first week we honed our observation skills, using Harrison (1985) as a major reference. Thereafter, we maintained almost constant watch during daylight hours (29 days during 9 September–31 October). Methods were based on those of the POBSP (King, 1970; Gould, 1974), modified by techniques utilized elsewhere (Tasker *et al.*, 1984; Haney, 1985; Gould & Forsell, 1989). The watch rotated between three observers (AKK, CBK, and DHE), with two observers on watch at all times. A change of one observer took place every hour on the hour, each person alternating 2-hour watches with a 1-hour break to reduce fatigue. Observations began 10–15 min before sunrise and terminated 10–15 min after sunset. Because we did not have dedicated ship time, observations were interrupted by periodic oceanographic sampling stations, during which time no seabird counts were made. Counts were not conducted within 10 km of oceanic islands where we landed (Christmas Island, Caroline Atoll, and Tarawa), but were made close to land in the Bohol, Sulu, and South China Seas.

Our ship speed averaged 15 knots during observations, higher than the 10 knots that Gould & Forsell (1989) consider ideal. At this time of year in the tropical Pacific, our higher

speed did not cause identification problems because few species were found in large numbers. When approaching or leaving a sampling station, we interrupted observations if the ship was moving less than 5 knots.

Bird counts were contained within rectangular strips extending 400 m to each side of the ship. Observers stood left and right of the midline of the ship, counting all birds seen 400 m or less ahead of the ship on their side, to a line perpendicular to the ship's direction at their position. Thus each hour of observation represents the pooled records of two observers watching a combined strip 800 m wide. Data were recorded on standardized field forms using local time. The following information was included: identification (to species or subspecies when possible), number of birds per sighting, feeding flocks and other associations, flight direction, plumage (adult, juvenile, sex), and weather. Due to poor lighting or weather conditions, some birds were identified only to genus or family. All birds sitting, flying, or flushed within the transect were counted, and their different behaviors noted. No birds were collected. The ship's position (latitude/longitude) and speed were recorded at the beginning and end of each hourly observation period. Ship-following species were noted during position checks and intermittently during the watch and were recorded when first seen.

Because the visibility of different species at sea varies greatly, we subdivided the maximum 400 m transect width into 3 bands corresponding to the approximate detection distances of each species: 1. 100-m band—small species, ordinarily seen relatively close to the ship, includes shorebirds, storm-petrels, and Bulwer's petrel (*Bulweria bulweri*); 2. 30-m band—gadfly petrels, shearwaters, most larids, and anatids, and 3. 400 m band, large or conspicuous species such as boobies, frigatebirds,

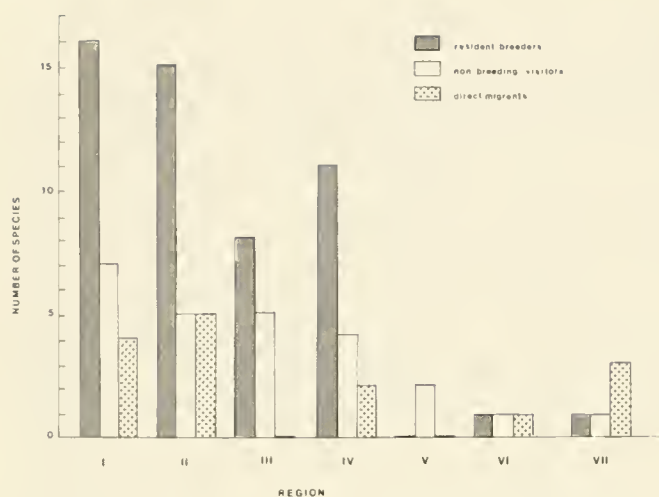


Fig. 3. Status of bird species observed along the cruise track of the R/V *Akademik Korolev*, 15 September–31 October 1988. Nonbreeding visitors and migrants migrate north or south to breed.

tropicbirds, and white terns (*Gygis alba*). These different detection distances were used as a basis for calculating the densities and area coverages for each different species (Hunt *et al.*, 1981; Briggs *et al.*, 1987). For ease of comparison within regions and with previous studies (King, 1970; Tasker *et al.*, 1984) and because the number of birds normally seen in tropical seas is lower than that observed in colder waters, bird densities were calculated in 3 ways: number/hour (per 2 observers), number/10 linear km, and number/10 km². In this paper, numbers/10 km² are used for comparison between species and regions; the other 2 calculated values are reported in Table 2.

Prior to the expedition, we examined skins of Pacific seabirds at the US National Museum, Washington, DC, focusing on variable, polymorphic, and particularly difficult species to identify. Terminology used in this paper follows the American Ornithologists' Union Check-list (AOU, 1983, 1985). The order of species within families, and alternate English names, follow Harrison (1985).

Results

Forty-six species (or field-recognizable subspecies) were observed along the 14,892-km cruise track of the R/V *Akademik Korolev* from 15 September to 31 October 1988 (Figs. 1,2). These were represented by members of 11 families of seabirds (including gulls, terns, and skuas), shorebirds (including phalaropes), and ducks (Table 3).

The most abundant species was the sooty tern (*Sterna fuscata*), accounting for 62.8% of the total number of birds (Fig. 3), but restricted to Regions I through IV. Noddy tern (*Anous* sp., primarily brown noddy, *A. stolidus*), wedge-tailed shearwater (*Puffinus pacificus*), and white tern followed as the next most frequently observed species. We observed birds belonging to the following three broad groupings (Fig. 3, Table 4):

a) Resident breeders. Seabirds may or may not have annual breeding cycles, which affects the temporal patterns of their dispersion at-sea. Within an archipelago, a species may exhibit asynchronous egg-laying periods on different islands or in separate colonies on the same island. For example, in the Line Islands, red-footed boobies (*Sula sula*) laid primarily

TABLE 2

Seabird densities along the cruise track of the R/V *Akademik Korolev*, 15 September–31 October 1988.

Region	Species	Number Birds		
		Per Hour	Per 10 Linear Km	Per 10 Km ²
I	Phoenix petrel	0.17	0.07	0.11
	Tahiti/Phoenix petrel	0.03	0.01	0.03
	Herald petrel	0.07	0.03	0.04
	White-necked petrel	0.10	0.04	0.07
	Cook's petrel	0.20	0.08	0.13
	Stejneger's petrel	0.06	0.02	0.06
	Bulwer's petrel	0.10	0.04	0.20
	Unidentified petrel	0.17	0.07	0.11
	Flesh-footed shearwater	0.03	0.01	0.03
	Wedge-tailed shearwater	1.37	0.53	0.88
	Sooty shearwater	0.50	0.19	0.32
	Christmas shearwater	0.13	0.05	0.09
	Audubon's shearwater	0.17	0.07	0.11
	Unidentified shearwater	0.10	0.04	0.07
	Unidentified shearwater/petrel	0.70	0.03	0.04
	Wilson's/Madeiran storm-petrel	0.37	0.14	0.72
	Leach's storm-petrel	0.03	0.01	0.08
	Unidentified storm-petrel	0.17	0.07	0.32
	Red-tailed tropicbird	0.13	0.05	0.07
	Masked booby	0.80	0.31	0.49
	Red-footed booby	0.13	0.05	0.07
	Brown booby	0.07	0.03	0.03
	Great frigatebird	0.17	0.07	0.01
	Bristle-thighed curlew	0.13	0.05	0.09
	Gray-backed tern	0.07	0.03	0.04
	Sooty tern	8.88	3.44	5.73
	Brown noddy	0.10	0.44	0.07
	Black noddy	0.17	0.07	0.11
	White tern	0.10	0.04	0.05
	Unidentified tern	0.03	0.01	0.03
II	Phoenix petrel	0.09	0.03	0.05
	Mottled petrel	0.05	0.02	0.03
	Herald petrel	0.05	0.02	0.03
	White-necked petrel	0.32	0.11	0.17
	Cook's petrel	0.14	0.05	0.08
	Bulwer's petrel	0.09	0.03	0.16
	Unidentified petrel	0.09	0.03	0.05
	Flesh-footed shearwater	0.05	0.02	0.03
	Short-tailed shearwater	0.05	0.02	0.03
	Wedge-tailed shearwater	0.32	0.11	0.17
	Sooty shearwater	0.09	0.03	0.05
	Christmas shearwater	0.05	0.02	0.03
	Little shearwater	0.05	0.02	0.03

TABLE 2 - continued

Region	Species	Number Birds		
		Per Hour	Per 10 Linear Km	Per 10 Km ²
	Audubon's shearwater	0.05	0.02	0.03
	Unidentified shearwater	0.09	0.03	0.05
	Unidentified shearwater/ petrel	0.05	0.02	0.03
	Leach's storm-petrel	0.09	0.03	0.16
	White-throated storm-petrel	0.09	0.03	0.16
	Red-tailed tropicbird	0.05	0.02	0.02
	Masked booby	0.32	0.11	0.13
	Red-footed booby	0.05	0.02	0.02
	Great frigatebird	0.73	0.24	0.30
	Lesser golden-plover	0.05	0.02	0.08
	Gray-backed tern	3.66	0.12	0.20
	Sooty tern	77.91	25.96	43.27
	Brown noddy	0.09	0.03	0.05
	White tern	0.73	0.24	0.31
III	Herald petrel	0.56	0.02	0.03
	Cook's petrel	0.06	0.02	0.03
	Bulwer's petrel	0.11	0.04	0.20
	Unidentified petrel	0.34	0.11	0.18
	Wedge-tailed shearwater	0.50	0.16	0.27
	Unidentified shearwater/ petrel	0.17	0.05	0.09
	Leach's storm-petrel	0.22	0.07	0.36
	Masked booby	0.28	0.09	0.11
	Ruddy turnstone	0.06	0.02	0.08
	South polar skua	0.06	0.02	0.03
	Sooty tern	7.39	2.40	4.00
	Brown noddy	13.11	4.26	7.09
	Black noddy	0.06	0.02	0.03
	Unidentified noddy	0.17	0.05	0.09
	White tern	4.94	1.60	2.01
IV	Kermadec petrel	0.05	0.02	0.03
	Bulwer's petrel	0.47	0.02	0.80
	Flesh-footed shearwater	0.05	0.02	0.03
	Wedge-tailed shearwater	4.98	1.76	2.93
	Unidentified shearwater/ petrel	0.14	0.05	0.08
	Wilson's/Madeiran storm-petrel	0.02	0.01	0.04
	White-tailed tropicbird	0.91	0.32	0.40
	Red-footed booby	0.84	0.30	0.37
	Brown booby	0.05	0.02	0.02
	Great frigatebird	0.02	0.01	0.01
	Northern shoveler	0.02	0.01	0.01
	Lesser golden-plover	0.05	0.02	0.08
	Sharp-tailed/pectoral sandpiper	0.12	0.04	0.20
	South polar skua	0.09	0.03	0.05
	Parasitic jaeger	0.05	0.02	0.03
	Unidentified skua	0.14	0.05	0.08
	Black-naped tern	0.02	0.01	0.01
	Sooty tern	4.70	1.66	2.77
	Brown noddy	4.21	0.15	0.03
	Unidentified noddy	4.68	1.65	2.75
	White tern	0.87	0.31	0.38

TABLE 2 - continued

Region	Species	Number Birds		
		Per Hour	Per 10 Linear Km	Per 10 Km ²
V	Streaked shearwater	0.44	0.17	0.28
	Wedge-tailed shearwater	1.53	0.59	0.99
	Unidentified shearwater	0.07	0.03	0.05
	White-tailed tropicbird	0.15	0.06	0.07
	Lesser golden-plover	0.15	0.06	0.28
	Black-naped tern	0.07	0.03	0.05
	White tern	0.07	0.03	0.04
VI	Wedge-tailed shearwater	0.14	0.03	0.08
	Great frigatebird	0.07	0.03	0.03
	Red-necked phalarope	0.76	0.27	1.36
	Pomarine jaeger	0.07	0.03	0.04
	Unidentified tern	0.07	0.03	0.04
	Unidentified gull/tern	0.14	0.05	0.08
VII	Masked booby	0.05	0.02	0.02
	Brown booby	0.25	0.09	0.11
	Unidentified frigatebird	0.98	0.04	0.05
	Red-necked phalarope	1.61	0.06	2.96
	Pomarine jaeger	0.10	0.04	0.07
	Parasitic jaeger	0.15	0.05	0.09
	Unidentified skua	0.29	0.11	0.19
	Caspian tern	0.25	0.09	0.15
	Bridled tern	0.15	0.05	0.09
	Crested tern	0.10	0.04	0.07
	Unidentified tern	0.25	0.09	0.15

from May to June on Christmas Island in 1965 (Clapp, 1967) but from August to November on Caroline Atoll (Kepler *et al.*, Subchapter 1.2, this volume) data indicated an egg peak from August to November. Other species disperse variable distances from their colonies during the breeding cycle. The case of Audubon's shearwater (*P. lherminieri*) was particularly interesting. Generally seen within 180 km of its breeding grounds, we found a bird 1,100 km away from its nearest known colony, Christmas Island, but approximately 400 km from Malden, a little-known island that has unexplored potential habitat for Audubon's shearwaters. Our data also included range extensions of resident breeders. For example, the wedge-tailed shearwater, the most abundant shearwater in the Pacific, has rarely been recorded west of 180° in the Caroline Islands (Micronesia), Philippine Sea, and southeast Asia, yet 84% of our sightings (N = 245) occurred in this area.

b) Nonbreeding visitors. These seabirds tend to be highly seasonal in their postbreeding movements. We observed birds that breed from the arctic to the antarctic. For example, Cook's petrels (*Pterodroma cooki*) breed on islands in temperate waters of the South Pacific, then undergo long transequatorial migrations into tropical and north temperate waters to spend their austral winter. Because of the enormous distances of such migrations, and because the distributions of birds are still poorly known in some regions, our data added range extensions for Kermadec petrel (*P. neglecta*) and little shearwater (*P. assimilis*).

TABLE 3

Seabird abundance by family along the cruise track of the R/V *Akademik Korolev*, 15 September–31 October 1988.

Family	Regions *							Total
	I	II	III	IV	V	VI	VII	
Total No. Birds	457	1,796	495	799	34	20	67	3,668
No. Species	26	24	13	18	6	3	8	
Procellariidae	117	35	22	243	28	2	-	447 (12.19%)
Hydrobatidae	17	4	4	1	-	-	-	26 (0.71%)
Phaethontidae	4	1	-	39	2	-	-	46 (1.25%)
Sulidae	30	8	5	38	-	-	6	87 (2.37%)
Fregatidae	5	16	-	1	-	1	2	25 (0.68%)
Anatidae	-	-	-	1	-	-	-	1 (0.03%)
Charadriidae	-	1	-	2	2	-	-	5 (0.14%)
Scolopacidae	4	-	1	5	-	-	-	10 (0.27%)
Phalaropodidae	-	-	-	-	-	11	33	44 (1.20%)
Stercorariidae	-	-	1	12	-	1	11	25 (0.68%)
Laridae	280	1,731	462	457	2	5	15	2,952 (80.48%)

* For geographic limits of each region, see Figs.1 and 2.

TABLE 4

Seabird species abundance along the cruise track of the R/V *Akademik Korolev*,
15 September–31 October 1988.

Species	No. Birds Seen							Total	Status
	Region								
	I	II	III	IV	V	VI	VII		
FAMILY PROCELLARIIDAE								447	
Phoenix petrel (<i>Pterodroma alba</i>)	5	2						7	RB
Tahiti/phoenix petrel (<i>Pt. rostrata/alba</i>)	1							1	RB
Mottled petrel (<i>Pt. inexpectata</i>)		1						1	MS
Kermadec petrel (<i>Pt. neglecta</i>)				2				2	WMS
Herald petrel (<i>Pt. arminjoniana</i>)	2	1	1					4	WMS
White-necked petrel (<i>Pt. externa</i>)	3	7						10	WMS
Cook's petrel (<i>Pt. cooki</i>)	6	3	1					10	WMS
Stejneger's petrel (<i>Pt. longirostris</i>)	2							2	MS
Bulwer's petrel (<i>Bulweria bulweri</i>)	3	2	2	20				27	RB
Unidentified petrel	5	2	6					13	
Streaked shearwater (<i>Calonectris leucomelas</i>)					6			6	WMN
Flesh-footed shearwater (<i>Puffinus carneipes</i>)	1	1		2				4	MS
Wedge-tailed shearwater (<i>P. pacificus</i>)	41	7	9	213	21	2		293	RB
Sooty shearwater (<i>P. griseus</i>)	15	2						17	MS
Short-tailed shearwater (<i>P. tenuirostris</i>)		1						1	MS
Christmas shearwater (<i>P. nativitatis</i>)	4	1						5	RB
Little shearwater (<i>P. assimilis</i>)		1						1	MS
Audubon's shearwater (<i>P. lherminieri</i>)	5	1						6	RB
Unidentified shearwater	3	2			1			6	
Unidentified shearwater/petrel	21	1	3	6				31	
FAMILY HYDROBATIDAE								26	
Wilson's/Madeiran storm-petrel (<i>Oceanites oceanicus/Oceanodroma castro</i>)	11			1				12	WMS
White-throated storm-petrel (<i>Nesofregatta fuliginosa</i>)		2						2	RB
Leach's storm-petrel (<i>Oceanodroma leucorhoa</i>)	1	2	4					7	WMN
Unidentified storm-petrel	5							5	

TABLE 4 - continued

Species	No. Birds Seen							Total	Status
	Region								
	I	II	III	IV	V	VI	VII		
FAMILY PHAETHONTIDAE									46
Red-tailed tropicbird (<i>Phaethon rubricauda</i>)	4	1						5	RB
White-tailed tropicbird (<i>P. lepturus</i>)				39	2			41	RB
FAMILY SULIDAE									87
Masked booby (<i>Sula dactylatra</i>)	24	7	5				1	37	RB
Red-footed booby (<i>S. sula</i>)	4	1		36				41	RB
Brown booby (<i>S. leucogaster</i>)	2			2			5	9	RB
FAMILY FREGATIDAE									25
Great frigatebird (<i>Fregata minor</i>)	5	16		1		1		23	RB
Unidentified frigatebird							2	2	
FAMILY ANATIDAE									1
Northern shoveler (<i>Anas clypeata</i>)				1				1	WMN
FAMILY CHARADRIIDAE									5
Lesser golden-plover (<i>Pluvialis dominica</i>)		1		2	2			5	WMN
FAMILY SCOLOPACIDAE									10
Bristle-thighed curlew (<i>Numenius tahitiensis</i>)	4							4	WMN
Ruddy turnstone (<i>Arenaria interpres</i>)			1					1	WMN
Sharp-tailed pectoral sandpiper (<i>Calidris acuminata</i> / <i>C. melanotos</i>)				5				5	WMN
FAMILY PHALAROPODIDAE									44
Red-necked phalarope (<i>Phalaropus lobatus</i>)						11	31	44	WMN
FAMILY STERCORARIIDAE									25
South polar skua (<i>Catharacta maccormicki</i>)			1	4				5	WMS
Pomarine jaeger (<i>Stercorarius pomarinus</i>)						1	2	3	MN
Parasitic jaeger (<i>S. parasiticus</i>)				2			3	5	MN
Unidentified skua				6			6	12	
FAMILY LARIDAE									2,952
Caspian tern (<i>Sterna caspia</i>)							5	5	MN
Black-naped tern (<i>S. sumatrana</i>)				1	1			2	RB
Gray-backed tern (<i>S. lunata</i>)	2	8						10	RB
Bridled tern (<i>S. anaethetus</i>)							3	3	RB
Sooty tern (<i>S. fuscata</i>)	266	1,705	133	201				2,305	RB
Crested tern (<i>S. bergii</i>)							2	2	RB
Brown noddy (<i>Anous stolidus</i>)	3	2	236	18				259	RB
Black noddy (<i>A. minutus</i>)	5		1					6	RB
Unidentified noddy			3	200				203	
White tern (<i>Gygis alba</i>)	3	16	89	37	1			146	RB
Unidentified tern	1					1	5	7	
Unidentified gull						2		2	
Unidentified larid						2		2	
Totals	457	1,796	495	799	34	20	65	3,668	

RB = resident breeder in the tropical Pacific.

W = nonbreeding visitor " " " "

MS = migrant: south to temperate/antarctic breeding colonies.

MN = migrant: north " " /arctic " "

c) Direct migrants. This grouping includes shorebirds (plovers, sandpipers, phalaropes) and ducks as well as seabirds. They move quickly through tropical waters from wintering grounds further north or south *en route* to breeding areas in the opposite hemisphere. Although some follow general routes and can be predicted at certain times of year, the overall dearth of studies in certain portions of the Pacific leaves much to be learned of their at-sea distribution. For example, Stejneger's petrel (*P. longirostris*) migrates from Chile to Japan, yet sightings had been scant in between before this expedition.

Species Accounts

Family Procellariidae

Shearwaters and petrels provided the greatest species diversity (17) of any family. Seven breed and disperse within the tropical Pacific, 11 breed in the temperate South Pacific and migrate to wintering grounds in the North Pacific, and 1 breeds in the temperate North Pacific and migrates south to winter (Table 4).

Although we did not encounter large migrating flocks, this family ranked second in total numbers seen (447; Table 3) and was particularly abundant in Regions I and II (Line and Phoenix Islands), after which species richness declined markedly to the west (Table 4). The western limit of procellariids (wedge-tailed shearwaters) was the Sulu Sea (08°47'N, 121°28'E).

Densities of individual species ranged from the rarer migrants at 0.03 birds/10 km² (Table 2) to the widespread resident breeder, wedge-tailed shearwater, whose numbers peaked in the Line Islands at 0.88 birds/10 km². Several species contributed to feeding flocks (Table 5), accounting for 10% of their participants.

Phoenix Petrel (*Pterodroma alba*): All seven of this rather uncommon species were sighted in Regions II and III, within its relatively small range in the central Pacific. Phoenix petrels sighted in the Line Islands were either within 1,200 km of their breeding grounds at Christmas Island or flying west toward colonies in the Phoenix Islands. Their highest densities were in the Line Islands (0.11/10 km²). None associated with other birds or participated in feeding flocks.

Tahiti/Phoenix Petrel (*Pterodroma rostrata* or *alba*): One *Pterodroma* found slightly east of Malden Island (central Line Islands) was either a Tahiti or a Phoenix petrel, look-alikes difficult to distinguish in the field. Tahiti petrels breed in the Society and Marquesas Islands, 800 km and 1,670 km, respectively, from its observed position.

Mottled Petrel (*Pterodroma inexpectata*): A single bird was seen flying southeast near Birnie Island (Phoenix Group) on 4 October. This species breeds in New Zealand during the austral summer, so this individual was likely migrating south from its winter quarters in the North Pacific. Its density in Region II was 0.03/10 km².

Kermadec Petrel (*Pterodroma neglecta*): The Kermadec petrel breeds in several island groups just south of the Tropic of Capricorn from Lord Howe Island to the coast of Chile. Formerly considered sedentary, recent records indicate that it ranges widely into the North Pacific (Gould & King, 1967;

Amerson, 1969; Harrison, 1985; Bailey *et al.*, 1989). Several records exist for the area extending from just south of Hawaii to the Marshall and Phoenix Groups. An old record from Duke-of-York Island (Bismarck Archipelago) indicates that this species may also occasionally straggle almost to New Guinea (King, 1970).

Kermadec petrels are not listed for the Gilbert Islands (Amerson, 1969) nor for any of the Caroline Islands (Pratt *et al.*, 1987); hence, the following observations extend the known range for this species: 2 Kermadec petrels (1 light and 1 dark phase) were seen on the morning of 12 October at the far eastern edge of Micronesia (04°03'N, 163°30'E), approximately 157 km south of Kosrae. The dark-phase petrel was flying directly south, while the light-phase bird had joined a feeding flock of over 200 sooty terns mingled with small numbers of wedge-tailed shearwaters, Bulwer's petrels and south polar skuas (*Catharacta maccormicki*). Kermadec petrels were seen only in Region IV with a density of 0.03/10 km².

Herald Petrel (*Pterodroma arminjoniana*): The Pacific breeding range of this medium-sized gadfly petrel includes Easter Island, the Pitcairn Islands, Tuamotus, Marquesas, Gambiers, and, further west, Tonga and Chesterfield (Coral Sea). In the nonbreeding season, herald petrels remain primarily in the Southern Hemisphere, occasionally wandering north of the equator (Harrison, 1985; Bailey *et al.*, 1989) where they are typically observed more than 150 km from land (King, 1970). We observed four adults (three dark phase, one light) in the Line, Phoenix, and Gilbert Groups. Two occurred just outside, the others within, the known pelagic range of this species (Harrison, 1985). The two dark-phase birds, beyond the eastern borders of their known range (05°24'N, 156°60'W), were flying southwest on 2 October (ca. 380 km east of Washington Island, Line Group). Densities were highest in the Line Islands (0.04/10 km²). Three of the birds were flying directly southwest.

White-necked Petrel (*Pterodroma externa*) (includes both *P. e. externa* and *P. e. cervicalis*): We observed 10 of these gadfly petrels: 3 occurred in September and October within their main wintering grounds in the central Pacific between the equator and Hawaii (0.07/10 km²), and 7 spanned the Phoenix Group, where densities were highest (0.17/10 km²). They are known to be abundant in the former location from May to November (King, 1967).

There are two subspecies that breed on opposite sides of the temperate Pacific: the white-necked (*externa*) in the Kermadec Islands northeast of New Zealand, and the Juan Fernandez (*cervicalis*) in the Juan Fernandez Islands of Chile. Seven birds were flying south or southwest (four flew together), presumably returning to breed on southern temperate islands during the austral summer.

Cook's Petrel (*Pterodroma cooki*): Cook's petrel breeds in the austral summer in New Zealand and the Juan Fernandez Islands. Although this transequatorial migrant ranges widely between the south and north temperate Pacific as far as the Aleutian Islands, its pelagic movements are not fully understood. Few records exist from the central Pacific. There are two records from the Phoenix Islands and sightings near the Hawaiian Islands in the northern spring (King, 1967; Harrison, 1985;

TABLE 5

Geographic Distribution of Flocks. "No. Birds" refers to the number of each species present in all feeding flocks of each region. Species are arranged according to their overall relative abundance in all feeding flocks. No flocks were seen in Regions V–VII.

Species	Region							
	I		II		III		IV	
	Flocks	No. Birds	Flocks	No. Birds	Flocks	No. Birds	Flocks	No. Birds
Sooty tern	1	85	6	1,074	2	108	1	200
Noddy sp.							1	200
Wedge-tailed shearwater			1	1			3	189
Brown noddy			1	2	3	111		
White tern			3	6	4	20	1	18
Red-footed booby			1	1			1	30
Great frigatebird			2	7				
White-tailed tropicbird							1	4
Masked booby			1	3				
South polar skua							1	2
Stercorariid sp.							1	1
Audubon's shearwater			1	1				
Bulwer's petrel							1	1
Kermadec petrel							1	1
"Shearwater/petrel"							1	5
Totals	1	85	6	1,095	4	239	3	651

Pratt *et al.*, 1987). They have not been previously recorded from the Gilbert Islands (Amerson, 1969). Our records are as follows:

Line Islands. Single birds were seen on 15 September at 10°38'N, 156°16'W; 10°13'N, 156°19'W (flying north); 09°29'N, 156°26'W (with 2 Bulwer's petrels); 16 September at 06°16'N, 156°50'W (flying north); 04°55'N, 157°00'W (flying south); and on 19 September at 00°22'S, 156°37'W.

Phoenix Islands. All single birds flying south, as follows: 2 October at 06°29'S, 162°19'W; 3 October at 05°16'S, 166°53'W and 05°12'S, 167°06'W.

Gilbert Islands. One bird flying southeast on 7 October at 00°49'S, 179°10'E.

We observed 12 adults (10 on transect) between 15 September and 7 October 1988. Two had particularly pale plumage. Sightings occurred just north of and within the Northern Line Group, where densities were highest (0.13/10 km²), in the Phoenix Group, and east of the Gilbert Islands. Of seven birds flying in a direct compass direction, four from the Line and Phoenix Islands were flying south, and one from the Gilbert Islands was flying southeast. Thus 71% of individuals of this species were flying in the approximate direction of their New Zealand breeding grounds, when such movements are expected. Only one Cook's petrel was associated with other birds (two Bulwer's petrels).

Stejneger's Petrel (*Pterodroma longirostris*): We observed two adult Stejneger's petrels in the Northern Line Group

(05°56'N, 156°53'W; 06°24'N, 156°50'W) on 16 September 1988, about 170 km east of Palmyra Atoll. There are few central Pacific records; POBSP personnel saw some near the Phoenix Islands (King, 1967), although this is not mapped in Harrison (1985). There appear to be no records of Stejneger's petrel between Hawaii and the Phoenix Islands.

Additional sightings were made during the ICBP 1990 Line and Phoenix Islands Expedition (ICBP, 1990; Kepler, 1990). We observed no Stejneger's petrels in the Line Islands during March and April but saw several birds heading north in the same area during May (11° to 15°S, 149° to 151°W).

Bulwer's Petrel (*Bulweria bulweri*): This species was relatively common (N = 27) throughout the four regions of the Pacific covered by the cruise. Because of its small size, it was only counted within 100 m of the ship (see Methods). Since this species breeds and ranges at widely-scattered locations in the Central and western Pacific, all our observations fell within its expected range, Regions I through IV. Three-quarters of our sightings were in Micronesia, primarily south of Kosrae and north of Ulithi Atoll. None were seen west of Yap (139°E). The major Bulwer's petrel breeding grounds in the northwest Pacific (Bonin, Volcano, islands of Taiwan and China) are well north of Micronesia, and Bulwer's petrel is regarded as a species whose numbers decrease gradually with increasing distance from land (King, 1970). Breeding occurs from April to September (King, 1967). Of our early October birds, equal numbers were heading either north or south.

The overall density of Bulwer's petrel in Micronesia was 0.80/10 km², four times the density encountered in Regions I through III (Line, Phoenix and Gilbert Islands).

Streaked Shearwater (*Calonectris leucomelas*): This large shearwater breeds on coastal islands off China, Japan and Korea and is known to travel southward during October and November toward its main wintering area in the New Guinea–northern Australia area. We observed six individuals, all from 18–20 October in the far western Pacific close to the Philippines (Region V). Two were recorded as having darker plumage. Sightings were restricted to a very narrow band of ocean between 130°15' and 135°14'E longitude. These were probably postbreeding migrants: three (50%) were flying due south, and all were solitary.

Flesh-footed Shearwater (*Puffinus carneipes*): Flesh-footed shearwaters breed during the austral summer on islands off Australia and New Zealand, and winter in the North Pacific north of the subtropical convergence. We observed four flesh-footed shearwaters in Regions I, II and IV, all migrating birds retruning to the south temperate Pacific to breed. Two were in the central Pacific south of Hawaii and in the Phoenix Islands, where the species has been reported in very small but regular numbers during the migration months, October to April (King, 1967). The rest occurred in a more expected sector of the western Pacific, although in a relatively narrow swath (05°12'S to 03°59'N, 164°08'E to 163°46'E), viz. between the western Gilbert and far eastern Caroline Islands. The densities of these transequatorial migrants were equal throughout (0.03/10 km²).

Wedge-tailed Shearwater (*Puffinus pacificus*): The wedge-tailed shearwater has long been considered the most common widespread shearwater of the southwest Pacific (Mayr, 1945; Jenkins, 1979). This species accounted for 8% of our total sightings (Fig. 4). It breeds on numerous islands throughout most of the tropical and subtropical Pacific from eastern Australia to Mexico south to the Pitcairn Islands. We observed 293 individuals, 213 (73%) of which occurred in Micronesia. The two largest concentrations, of 150 and 22 birds, both occurred on 13 October near Pohnpei. Our sightings ranged from immediately south of Hawaii through the Line, Phoenix, and Gilbert Islands, Micronesia, and the Philippine Islands to the far western edge of its range at 121°28'E longitude.

Although the pelagic distribution of this species is well known for the central and eastern Pacific regions and Marshall Islands (King, 1967, 1970, 1974b; Amerson, 1969), observations are surprisingly scarce in the Carolines–Belau–Philippine region (King, 1974b:63, 93). For this reason, we discuss our records in waters west of 180° longitude (Table 6), where 84% (N = 245) of our wedge-tail sightings occurred:

a) **Gilbert Islands** (Region III, 180–165°E). Although wedge-tailed shearwaters are known from this area (Harrison, 1985), we have been unable to find records of specific sightings in a detailed summary of published data on wedge-tailed shearwater distribution (King, 1974b). They are not listed, even as visitors, in the Gilbert Islands by Pratt *et al.* (1987) or Amerson (1969).

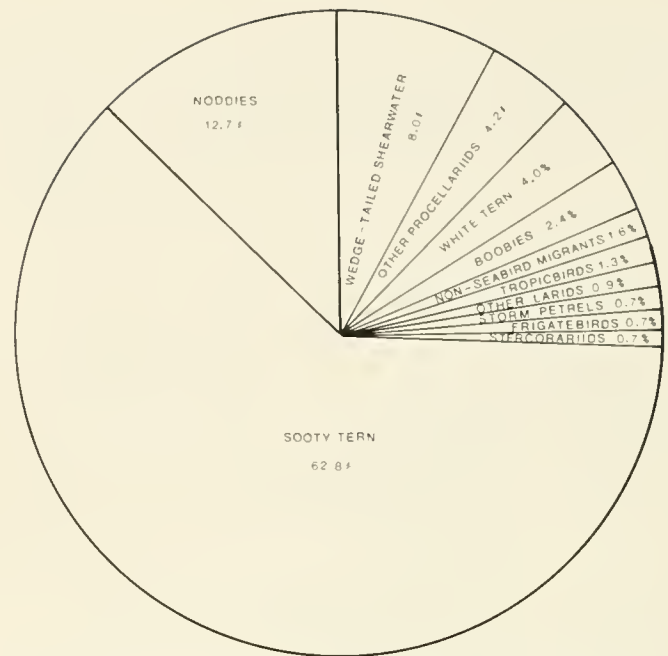


Fig. 4. Relative abundance of species or species groups on the cruise track of the R/V Akademik Korolev. Total number of birds seen was 3,668, belonging to 11 different families.

Although a resident breeder on several of the northern Marshall Islands (Amerson, 1969), the closest recorded sightings to the Gilbert Islands are 10 dark-phase birds seen on 2 November 1960 at Jaluit Atoll, southern Marshall Islands (Morzer Bruyns, 1965:58) and between 04°00' and 02°30'S, 169–155°E in October 1951 southwest of the Gilberts between Niutao Atoll and the Admiralty Islands (MacDonald & Lawford, 1954). These latter birds were reported as possibly *P. carneipes*, which has a totally different flight pattern. Our nine sightings were close to the equator at 179°E longitude, approximately 300 km north-northeast of Arorae Island. All birds were flying south.

b) **Micronesia** (Region IV, 165–136°E). Although known to be resident breeders in the northern Marshall Islands (Amerson, 1969:295) and central Carolines (Murphy, 1951:9), pelagic records of wedge-tails are sparse (King, 1974b:93). Breeding colonies are also difficult to locate. Pratt *et al.* (1987) state that this species is rare in western Micronesia: the westernmost record at these latitudes is evidently 150°E (District of Truk).

We observed wedge-tailed shearwaters (N = 213) throughout the Caroline chain of islands east to 132°59'E longitude: 73% of wedge-tails observed on our cruise were in this region.

c) **Philippine Sea and Basin** (Region V, 136–125°E). Of 21 wedge-tailed shearwaters seen west of 150°E (east of the Philippines and ca. 450 km north of Belau), all were dark phase (Table 6). Those in direct flight were heading either south or west. This species may visit Belau more frequently than records indicate. Owen (1971) does not mention its occurrence, although Pratt *et al.* listed it as a visitor. The overall density of

wedge-tails in this area, generally depauperate in seabirds, was 0.99 birds/10 km², far higher than for any of the other five species seen there.

d) Philippine Islands (Region VI, 125–117°E longitude). Our October observations confirm the presence of this species in the Sulu Sea (Delacour & Mayr, 1946; MacDonald & Lawford, 1954), where we saw two dark-phase adults flying south (0.08/10 km²).

e) Color Morphs, Flight Directions, and Densities. Pacific Ocean Biological Survey Program studies revealed much about the migratory movements of the wedge-tailed shearwater in the central and eastern Pacific (King, 1967, 1970, 1974b). In general, the dark-phase population predominates south of 10°N latitude, the approximate area covered by the east-flowing Equatorial Countercurrent and west-flowing South

Equatorial Current. Dark-phase birds move northward following the currents during the northern summer, reversing their movements in the fall.

Dark-phase birds observed during October would be expected to be heading south: of 39 individuals of known flight direction, 31 flew south and 4 southwest, toward the nutrient-rich waters of the Equatorial Countercurrent upwelling between 4°N and 9°N latitude (King, 1974a,b). Our largest concentration of wedge-tails was near Pohnpei (06°N, 157°E), contributing to the highest daily density of this species (10.95 birds/10 km²). At this time the sea was “boiling” with fish, which attracted a great variety of seabirds. Such densities of Wedge-tails are comparable to those within the countercurrent latitudes in the central Pacific (King, 1974a).

TABLE 6

Distribution, abundance, and behavior of wedge-tailed shearwaters west of 180°, Pacific Ocean and inland Philippine Seas, 7 October–23 October 1988.

Region	Lat.	Long.	Date	Nearest Island or Group	No. Birds	Overall Density (birds per 10 km ²)	Phase	Flight Behavior	Direction
III	01°00'S-02°55'N	180°00'-165°00'E	10/7-10/11	Gilberts	9	0.27			
	00°49'S	179°10'E	10/7	Arorae	8		-	Directed flight	S
	00°49'S	179°10'E	"	"	1		-	"	S
IV	02°55'N-11°10'N	165°00'-136°00'E	10/11-10/17	Micronesia	213	2.93			
	03°53'N	164°08'E	10/12	Kosrae	1		Dark	Directed flight	S
	"	"	"	"	1		"	"	"
	"	"	"	"	1		"	"	"
	04°03'N	163°31'E	"	"	17		"	Feeding flock	-
	"	"	"	"	1		-	Directed flight	N
	04°30'N	161°57'E	"	"	7		-	"	S
	"	"	"	"	1		"	"	NE
	05°24'N	159°04'E	10/13	Pohnpei	2		Dark	Solo feeding	-
	05°32'N	158°37'E	"	"	1		-	Flushed by ship	-
	05°43'N	158°25'E	"	"	22		-	Feeding flock with 1 South Polar Skua	-
	06°02'N	158°06'E	"	"	1		-	Directed flight	NE
	06°17'N	157°51'E	"	"	150		-	Feeding flock: 7 spp., 408 birds	-
	06°28'N	157°41'E	"	(in sight)	1		Dark	Directed flight	S
	"	"	"	"	2		"	"	SW
	"	"	"	"	2		"	"	S
	06°38'N	157°31'E	"	"	2		"	"	SW
	08°59'N	155°11'E	10/14	Murilo (Hall Is.)	1		"	"	S
V	11°10'-10°00'N	136°00'-125°00'E		Yap, Belau	21	0.99			
	11°02'N	135°19'E	10/18	320 km NW of Yap, 400 km NNE of Belau	2		Dark	Directed flight	S
	11°00'N	134°36'E	"	Belau	1		"	"	S
	"	"	"	"	2		"	"	W
	"	"	"	"	1		"	"	S
	"	"	"	"	1		"	"	"
	11°00'N	132°59'E	10/19	"	3		"	"	W
	"	"	"	"	10		"	Circling	-
VI	11°00'N	132°59'E	10/19	Belau	1	0.99	Dark	Directed flight	S
	10°00'N	125°00'-117°00'E		Philippines (Sulu Sea)	2	0.08			
	08°49'	121°44'	10/22	Negros, Mindanao	1		Dark	Directed flight	S
	08°47'	121°28'	"	"	1		"	"	S

Dark-phase birds accounted for 97% of sightings where color phase was noted (57). Only two light-phase individuals were seen (Region I, 10°46'N and 06°45'N), both south of Hawaii, where the majority of the population is light phased.

Short-tailed Shearwater (*Puffinus tenuirostris*): A wide-ranging transequatorial migrant, with movements and breeding phenology similar to those of the flesh-footed and sooty shearwaters (*P. griseus*), this species breeds off southeastern Australia and winters off the west coast of North America and the Bering Sea. We observed one adult (2 October) heading south through the eastern extremity of its known migratory pathway, the eastern Phoenix Islands (06°29'S, 162°19'W).

Sooty Shearwater (*Puffinus griseus*): Sooty shearwaters are wide-ranging, transequatorial migrants that breed from October to May in the Southern Hemisphere on islands off Australia, New Zealand, and Chile, migrating to equivalent high latitudes in the northern Pacific during the nonbreeding season. We observed very small numbers of birds on their annual southward migration. All 17 observations were in the south-central Pacific. We saw them on only 2 days: 16 September (N = 15), east of Washington Island (Line Group) and 2 October (N = 2), between Sydney and Starbuck Islands (east of the Phoenix Group). All were adults flying south, and none were feeding or associated with other species. Densities were 0.32 birds/10 km² in Region I and 0.05 birds/10 km² in Region II. Enormous flocks of migrants have been encountered in this area (King, 1967; CBK, personal observation).

Christmas Shearwater (*Puffinus nativitatis*): The Christmas shearwater, a year-round resident in the tropical Pacific, tends to remain fairly close to its breeding grounds all year, although it is generally seen more than 180 km from land (King, 1970). We observed four individuals in the Line Islands (05°N, 157°W) that were flying west, and a single bird in the Phoenix Group, flying north. Densities were low: 0.09 birds/10 km² (Line Islands) and 0.03 birds/10 km² (Phoenix Islands).

Little Shearwater (*Puffinus assimilis*): This small, distinctive "aukish" shearwater breeds and disperses within south temperate waters, generally only occurring at-sea north to 25°S latitude. However, its pelagic dispersal is not well known and wanderers have been recorded near the Marquesas, Marshall, and Hawaiian Islands (King, 1967). Clapp (1967) listed a doubtful record from Christmas Island in the late 1950's. We add a single straggler, seen on 4 October in the Phoenix Islands (03°59'S, 171°31'W) close to Birnie Island and flying north. Within 20 minutes, we also observed the similar Audubon's shearwater; both flew close to the ship, enabling us to compare size, bill length, and the degree of white present on the underwings.

Audubon's Shearwater (*Puffinus lherminieri*): This small shearwater is resident in the central and western Pacific: our five sightings (Regions I and II) were within its known range.

Our sightings of Audubon's shearwater at 02°N, 157°W were evidently from adjacent colonies on Christmas Island. However, we saw two birds flying northwest in the Southern Line Islands (06°32'S, 152°35'W) on 21 September 1988, approximately 1,100 km from Christmas Island and more than 1,800 km from Phoenix Island, the nearest known colonies

(Clapp, 1967; Stoddart, 1976; Garnett, 1983). Since this species usually ranges at sea within 180 km of its breeding islands (King, 1967), we speculate that an unknown colony lies within the Southern Line Islands. Malden Island, approximately 400 km distant from the Audubon's shearwaters in question, is a likely possibility. Little visited by biologists, approximately one-third of its interior is covered by a landlocked, supersaline lagoon with subterranean connections to the sea, containing a maze of interconnected islets and salt flats (Garnett, 1983; RNZAF, 1986). These islets have never been surveyed by ornithologists (R.B. Clapp, personal communication). They provide potential habitat for Audubon's shearwaters, since they resemble sites occupied by this species on Christmas Island. Bloxham (1925) recorded two species of shearwaters of unknown identity on Malden; Garnett (1983) proposes that one of them may have been Audubon's shearwater. Starbuck, another stark, arid guano island with a similar interior, is another probable source.

On 5 May 1990, a single Audubon's shearwater was observed flying north-northwest around 10°S, 155°W, approximately 640 km due south of Malden (ICBP, 1990), further suggesting the presence of a colony in the Southern Line Islands.

In Region II, we saw one Audubon's shearwater in a feeding flock at 03°57'S, 171°31'W, near a large breeding colony (ca. 12,000 birds) on Phoenix Island (Garnett, 1983).

Family Hydrobatidae

The storm-petrels were represented by three (possibly four) species (Table 4) and five unidentified individuals. Small numbers (N = 26) were present at sea from the Line Islands west to Micronesia. Wilson's/Madeiran storm-petrel in the Line Islands accounted for the greatest densities (0.72 birds/10 km²). Overall, storm-petrels accounted for 0.7% of the total number of birds on the cruise (Fig. 4). Typically solitary feeders, they never participated in feeding flocks. Our westernmost observation was of a Wilson's/Madeiran storm-petrel at 03°59'N, 163°45'E (south of Kosrae).

Wilson's Storm-Petrel (*Oceanites oceanicus*) and Madeiran (Harcourt's) Storm-Petrel (*Oceanodroma castro*): Wilson's storm-petrel breeds on subantarctic islands off South America and in Antarctica and ranges widely throughout all the world's oceans (Murphy, 1936; Murphy & Snyder, 1952). In the Pacific it migrates northward to wintering grounds within tropical and north temperate waters (Harrison, 1985). It is rarely seen in the Pacific except in the far east (King, 1967; Huber, 1971; Crossin, 1974). Records and sightings exist from the Marshall Islands, Solomons, New Hebrides, New Caledonia, waters close to Hawaii, the Phoenix Islands, and Christmas Island.

The Madeiran storm-petrel, although not congeneric with Wilson's, appears remarkably similar in the field. It is a resident breeder in the tropical Pacific; therefore, its dispersal range overlaps with the wintering areas of Wilson's, primarily west of the international date line.

Eleven Wilson/Madeiran storm-petrels were observed at 00°28'S, 156°32'W, east of Jarvis Island, flying southeast. A Wilson's, flying south, was located southeast of Kosrae

(04°03'N, 163°31'E). Huber (1971) has shown that Wilson's storm-petrels move through the Marshall Islands from April through September, sometimes in considerable numbers.

White-throated or Polynesian Storm-Petrel (*Nesofregata fuliginosa*): The white-throated storm-petrel is an uncommon central Pacific resident. We saw two (0.16 birds/10 km²) flying north on 5 October in the Phoenix Islands, 200 km northwest of the nearest land, McKean Island, where the world's largest population (1,000 birds) breeds (King, 1973). Approximately 500 birds also breed on nearby Phoenix Island, remaining in adjacent waters throughout the year, with limited dispersal eastward along the South Equatorial Current (Harrison, 1985).

Leach's Storm-Petrel (*Oceanodroma leucorhoa*): This species breeds at subarctic and temperate latitudes in the North Pacific, wintering primarily north of the equator. Its at-sea range is centered in the central Pacific, with greatest winter densities in a broad belt along the equator (Crossin, 1974). Our seven observations, all between 0 and 3°S latitude, fell within the known range of the species (i.e., the Line, Phoenix, and Gilbert Groups). Five were flying north, and two were flying southeast.

Family Phaethontidae

Tropicbirds were represented by two species observed in small numbers (N = 46) from the Line Islands west to the Carolines, including the Gilbert Islands. Most sightings were of solitary birds during the morning hours, up to 300 km from the nearest landfall. The highest density was that of the white-tailed tropicbird (*Phaethon lepturus*) in Micronesia (0.40 birds/10 km²), six times higher than elsewhere. Tropicbirds accounted for 1.3% of the total birds seen (Fig. 3, Table 3).

Red-tailed Tropicbird (*Phaethon rubricauda*): The red-tailed tropicbird ranges widely in the tropical and subtropical Pacific, breeding on many islands. Typically solitary, it is highly pelagic and is often observed many hundreds of kilometers from the nearest landfall (Harrison, 1985). Long-term studies have found that it is observed in roughly the same density regardless of distance from land (King, 1970).

We observed five individuals in Regions I and II between 17 September and 5 October. In the Line Islands, two occurred close to islands (Christmas, Malden). The remainder were approximately 300 km equidistant from Caroline, Malden, and Starbuck, all of which harbor small breeding colonies (Clapp, 1967; Gould *et al.*, 1974), although that on Caroline is the largest (Kepler *et al.*, Subchapter 1.2, this vol.). All birds were characteristically solitary; one was resting on the water. This was also found by POBSP, whose number of sightings exceeded one thousand: 87% of sightings were of lone birds, and 14% were sitting on the water (Gould *et al.*, 1974). Pacific Ocean Biological Survey Program found that birds were most commonly observed during morning hours: 80% of our birds were seen before 0820 h. All flying birds were adults flying south. One bird was observed in the Phoenix Islands approximately 300 km northwest of McKean Island, where some 500 breed (Gould *et al.*, 1974).

Densities were highest in the Line Islands (0.07 birds/10 km²). Such at-sea abundance is low, probably because the species was breeding. On Caroline Atoll, for example, eggs and chicks were present in late September (Kepler *et al.*, Subchapter 1.2, this vol.).

White-tailed Tropicbird (*Phaethon lepturus*): Like *P. rubricauda*, the white-tailed tropicbird is a resident breeder throughout the tropical Pacific. It is, however, less pelagic. Of the 41 individuals we observed, 38 were seen on 13 October, with Pohnpei in sight most of the day: most were alone or in groups of up to four or fewer. Maximum numbers were seen in the morning. Those seen with directed flight were generally traveling toward or away from Pohnpei. Ten (26%) were sitting on the water, and four had joined a large feeding flock. White-tailed tropicbirds favor high islands for nesting and are known to nest in trees and rocky cliffs on Pohnpei (Baker, 1951).

A single white-tailed tropicbird was sighted 400 km north of Belau, where it breeds on several islands (Baker, 1951). Our last sighting was of a lone bird on 21 October in Region V, on the far northwestern edge of the species' range (Harrison, 1985). It was flying east approximately 200 km east of Samar Island (Philippines) at 10°49'N, 127°53'E.

Family Sulidae

Boobies were seen throughout the study area except in Region V, the Philippine Sea and Basin. All three pantropical species were seen in the Line Islands only. Although we saw only 87 boobies, this family ranked third in total numbers, contributing 1.3% of all individuals observed on the cruise (Fig. 4, Table 3). It was most common in the Line Islands and Micronesia (Figs. 5,6; Table 3). Many sightings were within 80 km of their nearest breeding islands, but there were several exceptions, one being a possible new pelagic record of a masked booby (*S. dactylatra*) in the central South China Sea (see below).

All three species of boobies commonly participate in feeding flocks. This tendency is greatest with the red-footed booby (*S. sula*) but is much less overall than for more gregarious species such as sooty terns or wedge-tailed shearwaters (King, 1970). Our data (14 flocks) indicate that boobies participated in 21.4% of the flocks (Table 7), accounting for 1.6% of the total number of flocking birds (Fig. 7). Of 893 feeding flocks in a large study area centered on the Hawaiian Islands, boobies participated in 12.3%, although their numbers only accounted for 1.8% of the total (King, 1970).

Masked Booby (*Sula dactylatra*): Masked boobies, resident breeders in the tropical Pacific, were seen sporadically across the entire cruise track (N = 37). They were most common in the Line Islands, where densities reached 0.49 birds/10 km². Small numbers were present in the Phoenix and Gilbert Groups and South China Sea (Table 2). Although wide-ranging throughout the Pacific, this species was not mapped as occurring west of around 143°E (i.e., the Marianas chain) (Harrison, 1985) but is recorded elsewhere from the Philippines, coastal

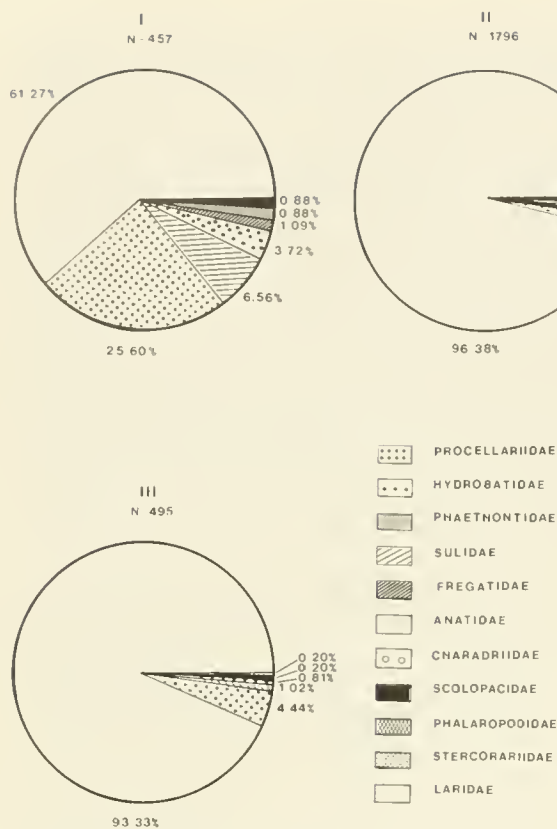


Fig. 5. Relative abundance of birds by family in Regions I-III.

Java, Indo-China, Malaya, and Borneo (Delacour & Mayr, 1946; King & Dickinson, 1975). There appear to be no records from the central South China Sea, where we saw a single juvenile, flying west, on 25 October at 05°49'N, 107°30'E, a location equidistant (ca. 400 km) from Borneo, Vietnam, and the Malay Peninsula.

Nonmigratory, masked boobies generally occur within the vicinity of their breeding islands, but they roam far out to sea. They characteristically follow ships: one-quarter of the birds circled around or followed the R/V *Akademik Korolev*. Juveniles-subadults accounted for two-thirds of our overall sightings, especially in the Line Islands, where they breed.

Red-footed Booby (*Sula sula*): This pantropical booby ranges across the entire tropical and subtropical Pacific, breeding in many localities. We observed 41 individuals in the Line, Phoenix, and Caroline Islands.

Although nonmigratory, the lack of subadult birds at some colonies has given rise to the hypothesis that although adults are relatively sedentary, many juveniles disperse from their natal islands (Schreiber & Ashmole, 1970). Pacific Ocean Biological Survey Program personnel have shown that red-foots generally remain within the vicinity of breeding or roosting areas, and that adults are seldom encountered more than 80 km from land (King, 1967). Our sightings conformed to this pattern. For example, we passed 300 km east of Palmyra, which harbors the largest colony of red-foots in the world (25,000), yet saw none. The only red-foots seen in the Line Islands were three light morph adults, flying east, within 110 km of Malden Island, where approximately 2,000 birds

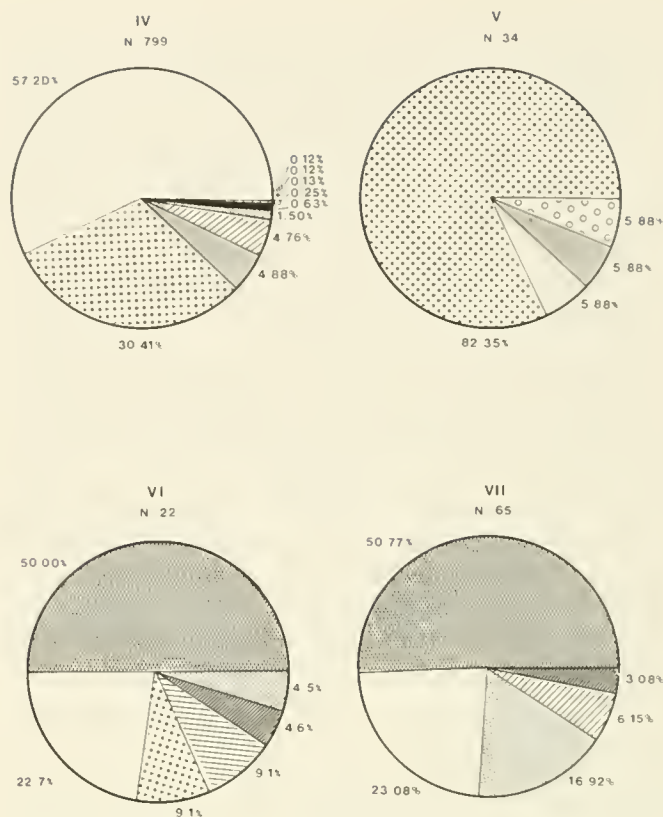


Fig. 6. Relative abundance of birds by family in Regions IV-VII. See Fig. 5 for legend.

TABLE 7

Participation by species or species groups in 14 feeding flocks along the 14.892 km cruise track.

Species	Flocks	Participation
	Number	Percent
Sooty tern	10	71.4
White tern	8	57.1
Noddies	5	35.7
Wedge-tailed shearwater	4	28.6
Other shearwaters and petrels	4	28.6
Boobies	3	21.4
Great frigatebird	2	14.3
Stercorariids	2	14.3
White-tailed tropicbird	1	7.1

breed (Clapp, 1967), and 1 juvenile, also flying east, around 460 km northwest of Caroline Atoll. In the Phoenix Group, we observed one dark morph adult in a feeding flock about 100 km equidistant from several islands.

In the central Pacific, red-foots lay from February to November, depending on the island and food supply (Nelson, 1978). In the Southern Line Islands, the major egg-laying period from 1988 to 1989 was September to October (ICBP, 1990; Kepler *et al.*, Subchapter 1.2, this vol.), which may have accounted for the small number of birds seen on our cruise. During March and May 1990, at-sea observations throughout the Southern Line Islands recorded much larger numbers of

red-foots than in September 1988. These were primarily juveniles dispersing after a successful breeding season.

On 13 October we observed 30 red-foots in the vicinity of Pohnpei. Most of these were participants in two feeding flocks, one of which was the second largest on the cruise. Both flocks developed immediately after a storm. The proportion of light-to-dark-phase birds at Pohnpei was 22:9. Red-foot density was highest on this day (1.62 birds/10 km²). Overall densities were 10 times greater in Micronesia than elsewhere, due to the large numbers seen feeding near Pohnpei.

Brown Booby (*Sula leucogaster*): This pantropical species ranges widely in the Pacific and breeds on almost every island group, although typically in smaller numbers than red-foots. The brown booby, less dependent on the tropical blue waters preferred by the other two species, is often found in inshore waters, including harbors and estuaries, which are more polluted and more accessible to man. Because of this, Nelson (1978) considers that the brown booby has suffered more than its congeners, probably accounting for their small numbers in populated areas such as Micronesia and the South China Sea. Brown boobies are seldom encountered more than 80 km from land (King, 1967), but Harrison (1985) noted that there is evidence to support small-scale dispersal.

We observed only nine individuals in the Line Islands, Caroline Islands (Micronesia), and South China Sea. We attempted to relate these individuals to nearby colonies. In the Northern Line Islands (two sightings at 02°02'N, 157°37'W) the closest colony was Christmas Island (N = 100), 32 km distant.

In Micronesia, the only brown boobies (two adults) were at 10°03'N, 150°02'E, approximately 150 km northwest of Magur, Namonuito Atoll, Truk (07°N, 147°E), and 220 km from uninhabited East Fayu Island, Truk (08°N, 151°E). Although brown boobies nest on uninhabited islands in the Marshall Islands (Amerson, 1969; SPREP, 1989), their colonies are rare and little known in the Caroline Islands. Some birds were seen at Truk in 1945 (Baker, 1951), and earlier this century, "incredible numbers of seabirds," which Nelson (1978) suspects may have included brown boobies, were reported on West Fayu, Gaspar Rico, and Magur. Nelson further notes that "East Fayu is also a breeding site," implying a colony of this species. Although the ornithology of these islands is virtually unstudied (NID, 1945; Nicholson & Douglas, 1969; Owen, 1971, 1977a,b; Ray Fosberg, personal communication), several colonies of brown boobies may still exist in the Caroline Islands. It is unlikely that the brown boobies we observed were from the Marshall Islands, the nearest known colony of which is Enewetak, about 1,400 km to the east.

Seabird information in the more remote islets of the Philippines and in the South China Sea is similarly scarce and outdated (Delacour & Mayr, 1946; King & Dickinson, 1975; Nelson, 1978; Harrison, 1985). Nelson states that "the status of the Brown Booby here is little known. There are some, could be many and may be few." Their only known nesting colony near Balabac Strait is at Tubbataha Reefs (68°N, 120°E) in the central Sulu Sea (Worcester, 1911, in Nelson, 1978, IUCN, 1988a).

In the South China Sea, we observed five brown boobies in the Balabac Strait close to numerous islands off the southern tip of Palawan (07°44'N, 116°58'E) and near northwest Borneo (05°92'N, 114°03'E and 04°40'N, 113°20'E). The closest known colony is Spratly Island (Nan-Sha Reefs), evidently the only remaining colony of brown boobies in Malaysian waters that has not been overexploited (Nelson, 1978) that was still extant 16 years ago (Haile, 1964, in Nelson, 1978). Both locations were within 30 km of coastlines. Our brown boobies, approximately 200 km west of this reef and flying east, could have originated there (or on several other little-known islands in the southwest Sulu Sea).

Overall densities of brown boobies were low everywhere, but were four to six times higher in the Sulu Sea–South China Sea than in the Line Islands and Micronesia, respectively (Table 2). These distributional patterns are most likely due to the proximity of our cruise track to potential breeding islands and nearshore waters. We saw no brown boobies in feeding flocks.

Family Fregatidae

Frigatebirds were seen throughout our cruise track except for the Gilbert Islands and the Philippine Sea. The only identifiable species was the great frigatebird (*Fregata minor*); two distant, unidentifiable frigatebirds were seen in the central South China Sea. Surprisingly, no lesser frigatebirds (*F. ariel*) were seen, even though they winter in the western tropical Pacific (Sibley & Clapp, 1967). Densities (Table 2) were highest in the Phoenix Islands (0.30 birds/10 km²), where the largest populations in the Pacific breed, and lowest in Micronesia, where frigates are known to be scarce. Overall, frigates accounted for only 0.7% of all birds observed on the cruise (Fig. 4).

Great Frigatebird (*Fregata minor*): We observed 23 great frigatebirds in the Line, Phoenix, and Caroline Islands. Densities were highest in the Phoenix Islands (Table 2), where over 30,000 are known to breed (Stoddart, 1976).

We saw only five great frigatebirds in the Line Islands, where around 13,000 breed (Clapp, 1967; Garnett 1983; Kepler *et al.*, Subchapter 1.2, this vol.). These low numbers may reflect the fact that birds are concentrated on and near colonies during the breeding season (Clapp, 1967; Kepler *et al.*, Subchapter 1.2, this vol.).

In Micronesia, we saw only one frigatebird, part of a large feeding flock near Pohnpei. Evidently frigatebirds are infrequent in the Caroline Islands (Baker, 1951; King, 1967; Pratt *et al.*, 1987). We located only one reference to breeding colonies of this species in this region (Niering, 1961); otherwise they "are probably resident, especially in the eastern part" (Baker, 1951).

The juvenile frigate in the southwest Sulu Sea (08°02'N, 117°28'W) and the adult in the South China Sea near Vietnam (05°48'N, 106°51'E) could have come from anywhere, as they may wander thousands of kilometers (Sibley & Clapp, 1967; Nelson, 1975). Great frigatebirds were minor participants in feeding flocks, contributing only 0.3% of the total numbers (Table 8).

Family Anatidae

Only one vagrant duck was observed (below), with an overall density in Micronesia of 0.01 birds/10 km².

Northern Shoveler (*Anas clypeata*): This Holarctic breeder is a rare but regular vagrant to Oceania. Recorded locations in Micronesia are the Marianas, Pohnpei east to Wake, and the Marshalls (Baker, 1951; Pratt *et al.*, 1987).

We saw an unsexed bird in eclipse plumage three times within a half hour on 13 October near Pohnpei. Each time it was flushed by the ship. Its characteristic bill shape and bicolored speculum made identification relatively easy.

Family Charadriidae

We observed only one member of this family in small numbers during its southward migration from arctic breeding grounds.

Lesser Golden-Plover (*Pluvialis dominica*): We saw five golden-plovers: Phoenix Islands, Caroline Islands (north of the Hall Islands and Ulithi Atoll), and in the Philippine Sea, where its density was highest (0.28 birds/10 km²).

This long-legged plover breeds in Siberia and arctic Alaska, migrating annually to islands throughout the tropical Pacific. Most abundant from August to April, small numbers are present all year (Pratt *et al.*, 1987). It is also a common migrant in southeast Asia (King & Dickinson, 1975).

During an oceanographic station on 19 October, one individual, uncaptured on the transects, circled the ship several times and landed, remaining on board for a week, during which time it weakened considerably. Its final attempt at flight resulted in drowning.

Family Scolopacidae

Ten members and three species of this family were observed, all present in small numbers scattered within the Line, Gilbert, and Caroline Islands. All were migrants from Holarctic breeding grounds.

Shorebirds are rarely seen in large numbers at sea, even during migration. For example, POBSP personnel on the *Townsend Cromwell*, working replicate tracks in a 171 million-ha study area from March 1964 to June 1965, observed only four species, each only once (King, 1970). Nonscaubird migrants (sandpipers, plovers, phalaropes, and a duck) observed from the R/V *Akademik Korolev* accounted for 1.6% of the total birds seen (Fig. 3).

Bristle-thighed Curlew (*Numenius tahitiensis*): One of the world's least-studied shorebirds, the bristle-thighed curlew is considered rare throughout its range and is a candidate for the US Fish & Wildlife Service Endangered Species List (Gill, 1990; Marks *et al.*, 1990). During the boreal winter, it is common in the Line Islands, northwest Hawaiian Islands, and southeast Polynesia but uncommon to rare elsewhere in the Pacific (Pratt *et al.*, 1987). All our at-sea sightings were on 16 September in the Northern Line Islands (density 0.09 birds/10 km²) clustered in a small area north-northeast of Fanning Island and close to Christmas Island (04°55'N to 02°02'N, 157°00'W to 157°37'W). Half the birds were flying south, the most expected direction for September, as curlews are most abundant in the Line Islands and Tuamotus between

October and April (Gill, 1990; Kepler *et al.*, Subchapter 1.2, this vol.). We saw no more until arriving on Caroline Atoll one week later, where we estimated a population of >300.

Ruddy Turnstone (*Arenaria interpres*): Another arctic breeder that winters in the Pacific, the ruddy turnstone is a widespread migrant to the Pacific, mostly between August and May. It is common from the Hawaiian Islands and Micronesia south to Samoa and Fiji (Pratt *et al.*, 1987). A single turnstone circled the ship in late afternoon about 80 km east of Abemama Atoll, Gilbert Islands, on 8 October.

Sharp-tailed (*Calidris acuminata*)/Pectoral Sandpiper (*C. melanotos*): These similar species are arctic breeders that winter in the South Pacific. We observed five birds in fall plumage flying south in a tight flock on 16 October at 11°10'N, 143°17'E. Both species have been recorded from Micronesia, especially *C. acuminata* in the western portion of the archipelago (Pratt *et al.*, 1987).

Family Phalaropodidae

One member of this family was found in the South China Sea, one of its favored winter quarters.

Red-necked Phalarope (*Phalaropus lobatus*): A circumpolar breeder, this phalarope migrates south to winter at sea. Although it can be encountered almost anywhere in the Pacific-southeast Asian region between the Aleutians and the equator, it favors two areas: coastal Peru and the South China Sea (Harrison, 1985).

We first observed small flocks of this species on 22 October on the eastern edge of the Sulu Sea (08°59'N, 123°12'E). They continued to appear thereafter, characteristically flushing from the water close to the ship's sides. Those that were not flushed were observed resting on the water surface or feeding in areas where currents or wind produced debris or foam lines.

We saw 44 phalaropes, 1.20% of the total number of birds on the cruise. Their highest density was in the South China Sea (2.96 birds/10 km²).

Family Stercorariidae

Three species of skuas/jaegers were seen (*N* = 13) plus 12 unidentified stercorariids (Table 4). They occurred primarily in Micronesia and the South China Sea, where densities were 0.16/10 km² and 0.35/10 km², respectively. None were seen in the Line and Phoenix Islands, or in the Philippine Sea and Basin (Regions I, II, V). Stercorariids accounted for 0.7% of all birds observed on the cruise.

Although ranging widely, movements of skuas and jaegers are little known except that some migratory pathways tend to follow coastlines (King, 1967). Some juveniles evidently remain on the wintering grounds all year.

Only the Pomarine jaeger has been recorded for southeast Asia (Tenasserim, Malaya, central Thailand, and Hong Kong) (King & Dickinson, 1987:153). However, King & Dickinson noted that three other species may occur there. We report possible first sightings of the parasitic jaeger in the South China Sea. Since all stercorariid sightings are rare for the western Pacific and southeast Asia, our data on 12 unidentified species follows:

- a) 12 October, two in feeding flock at 04°03'N, 163°31'E;
- b) 13 October, five flying north, one in feeding flock at 06°16'N, 157°51'E. Heavy squalls and winds from the north;
- c) 15 October, one flying east at 10°19'N, 147°39'E; and
- d) 25 October, six flushed by ship from resting position on water at 05°44'N, 108°01'E.

South Polar or McCormick's Skua (*Catharacta maccormicki*): This thickset, gull-like seabird breeds in Antarctica. It is an uncommon migrant in the Pacific, known only from the Hawaiian Line, and Phoenix Islands, possibly west to the Gilbert Islands (Pratt *et al.*, 1987). Harrison (1985) notes that juveniles disperse much further north than adults, possibly following a clockwise path across the Pacific rim past Japan (May–July) to British Columbia and California (September–October), then back to Antarctica to breed in the austral summer.

We observed five south polar skuas (three light- and one dark-phased adults and one juvenile) in Regions III and IV (Gilbert and Caroline Islands). All flew very close to the ship, and four participated in feeding flocks.

Our sightings fall within the known range of this species (Harrison, 1985), although other authorities indicate that south polar skuas do not range this far west (Mayr, 1945; Baker, 1951; Pratt, 1987). Since published records are sparse (they were not listed in Baker, 1951), our exact sightings follow:

- a) one juvenile, 8 October, flying south at 01°00'N, 172°40'E, just south of Tarawa, Gilbert Islands.
- b) two adults, light phase, 12 October, in a feeding flock at 04°03'N, 163°31'E, south of Kosrae. The feeding flock was composed of six species: two south polar skuas, two Pomarine/parasitic jaegers, >200 sooty terns, 17 wedge-tailed shearwaters (dark phase), 1 Kermadec petrel, 2 Bulwer's petrels. It developed in midmorning immediately after a series of rain squalls had moved through the area from the south.
- c) two adults (one very dark, one light), 13 October at 05°43'N, 15°25'E, just south of Pohnpei. The dark morph was flying southeast, the light one had joined a small feeding flock of 22 wedge-tailed shearwaters. Four hours later heavy winds and squalls hit us from the north, after which a massive concentration of fish attracted a large feeding flock which included an unidentified skua.

The highest densities of south polar skuas were in Micronesia (0.05 birds/10 km²).

Pomarine Jaeger or Pomarine Skua (*Stercorarius pomarinus*): This Holarctic-breeding jaeger migrates south to winter throughout the tropical, subtropical, and temperate areas of the Pacific. Evidently in good breeding years adults move south in August–September, followed by juveniles in September–October (Harrison, 1985). Our entire cruise track was within its known range.

From 22 to 25 October we observed three Pomarine jaegers in the Sulu Sea and South China Sea (Table 4). One was a light-phase adult, the rest, juveniles. One juvenile was flushed from a resting position on the water, while the others flew east or south. The highest densities of this species were in the South China Sea (0.07 birds/10 km²).

Parasitic Jaeger or Arctic Skua (*Stercorarius parasiticus*):

The Holarctic breeding and Pacific wintering ranges overlap those of the Pomarine Jaeger (Harrison, 1985). Since this species has not been recorded from the central Pacific and is uncommon in the western Pacific (for example Bismarck Archipelago and Bonin Islands), its migration routes are thought to remain close to the continental coasts (King, 1967). King & Dickinson (1975) mentioned that it might occur in southeast Asia.

Our observations came from the Caroline Islands and South China Sea. One juvenile was sighted on 12 October, south of Kosrae (04°22'N, 162°21'E) flying east; and one adult was seen on 14 October north of the Hall Islands (09°46'N, 154°43'E), flying southeast. We also saw parasitic jaegers on 24 October off the north coast of Borneo (04°40'N, 113°20'E, one juvenile, flying southeast) and on 25 October in the central South China Sea (05°49'N, 107°30'E, one adult dark morph, flying southwest).

Three of our five birds on transect were headed in a southerly direction, which is appropriate for October, when they dispersed south from their breeding grounds.

Greatest densities (Table 2) were in the South China Sea (0.09 birds/10 km²), which fits the hypothesis that migratory routes tend to follow continental coasts.

An additional parasitic jaeger was encountered during our 3-day layover near Mui Bai Bung Cape, Vietnam at 05°47'N, 107°45'E: On 27 October at 1605 ha juvenile, dark morph parasitic jaeger pursued an adult male shikra (*Accipiter badius*) with prey, a barn swallow (*Hirundo rustica*), for about 4 minutes (Ellis *et al.*, 1990). Finally the jaeger bound to the shikra and/or its prey. All three birds whirled about three revolutions and fell into the sea. After about 7 seconds in the water, the shikra flapped away. The jaeger remained in the water with its prize, drifting near the ship's stern. Oceanographers later found the swallow's head in a plankton net.

Family Laridae

This family was represented by 9 species of terns, plus 4 unidentified larids, totaling 2,953 individuals. Larids accounted for 81% of all birds sighted on the cruise. They dominated the pelagic waters of Regions I to IV, after which their numbers diminished considerably. Sooty terns (*Sterna fuscata*) were the most abundant species overall, accounting for 62.8% of all birds seen on the cruise (Fig. 3), with a maximum density of 43.27/10 km² in the Phoenix Islands.

Larids, which characteristically breed on oceanic islands (sooty tern, black and brown noddies, white tern), were present in far greater abundance than species that typically inhabit areas closer to continents (Caspian tern, *S. caspia*; black-naped tern, *S. sumatrana*; and bridled tern, *S. anaethetus*). We expected to see far more coastal birds in southeast Asia. Human population pressures and habitat alteration evidently weigh heavily on the natural resources in this area.

Sooty, white, and noddy terns were major participants in feeding flocks, accounting for 88.12% of all flocking birds (Table 5).

Caspian Tern (*Sterna caspia*): This large, cosmopolitan tern primarily breeds inland in Europe (including the Baltic Sea and interior USSR) and North America, along sea coasts and inland along rivers and lakes, migrating and dispersing southward during the nonbreeding season, remaining very close to continental coastlines. Apart from its winter status in Japan as a visitor, the Caspian tern is rare or uncommon in southeast Asia (Harrison, 1985; King & Dickinson, 1987); records are from Cambodia, Laos, extreme south Vietnam, and Thailand, but not from Singapore (Hails, 1987). We observed five Caspian terns, flying east and south, on the last day of the cruise, 31 October, in Singapore Roadstead. Absent elsewhere, this species had a density of 0.49 birds/10 km² here.

Black-naped Tern (*Sterna sumatrana*): A small, mostly white, rather delicate tern, the black-naped is mainly sedentary, breeding in the warm waters of the western Pacific and southeast Asia. It is primarily a resident of seacoasts and offshore islets (Harrison, 1985; King & Dickinson, 1987), extending eastward no further than 180° longitude (King, 1967).

We recorded two, one adult 80 km north of Uliihī Atoll (District of Yap, Micronesia) and a juvenile approximately 550 km east of the Philippines.

Gray-backed or Spectacled Tern (*Sterna lunata*): The gray-backed tern breeds in the Hawaiian, Phoenix, Line, and Tuamotu Islands, plus several other island groups to the southwest. At sea, it occurs as a vagrant or migrant within these approximate boundaries (King, 1967; Harrison, 1985). Their range is poorly known, probably because they are similar to, and often associated in small numbers with, the abundant sooty tern.

We recorded eight gray-backed terns in the Line and Phoenix Islands. Two adults were seen on 20 September within 30 km of Malden (04°03'S, 155°01'W). Within the Line Islands, gray-backed terns are known to breed on Christmas, Jarvis, and Malden (Clapp, 1967), thus we were probably observing birds from the Malden colony (500–1,000 birds), which would have been breeding at that time (Clapp, 1967; Grossman & Grossman, 1974; Garnett, 1983).

In the Phoenix Islands we saw two birds centrally in the group and six (including one juvenile) north of McKean. Gray-backed terns breed on Enderbury (N = 10,000 birds), Phoenix (N = 1,800 birds), and McKean (N = 23,000 birds) (King, 1973; Garnett, 1983).

Gray-backed tern densities were greatest in the Phoenix Islands (0.20 birds/10 km²), close to the largest breeding colonies in the world. Because breeding was in progress, most terns were likely to be on or near land.

Bridled or Brown-winged Tern (*Sterna anaethetus*): Frequenting offshore waters and open ocean in the tropics and subtropics, this species is the ecological counterpart of *S. lunata* in the western Pacific. We identified three bridled terns in Singapore Harbor; they are known to be offshore residents of the Malay Peninsula (Hails, 1987; King & Dickinson, 1987).

Sooty Tern (*Sterna fuscata*): The most abundant seabird in the tropical Pacific, the sooty tern breeds colonially in large numbers on almost every island group. It ranges widely between the tropics of Capricorn and Cancer.

We observed this species in the Line, Phoenix, and Gilbert Islands and Micronesia. It was the most abundant bird observed on the cruise (N = 2,305), nearly eight times more numerous than the secondmost common species, the wedge-tailed shearwater (Table 4). Sooty terns comprised 62.8% of the total number of birds observed (Fig. 4).

Sooty terns ranged throughout the Line Islands, with heavier concentrations near Christmas and Jarvis. Major colonies, of approximately two million each, exist on these two islands. The Christmas populations have declined drastically in recent years (from an estimated 15 million 10 years ago) due to predation by rats and cats, direct human exploitation for food, and reproductive failure due to the 1982–1983 El Niño Southern Oscillation (King, 1973; Gould, 1974b; Garnett, 1984; Schreiber & Schreiber, 1984; E. Schreiber, personal communication).

In Region II, sooty tern populations are estimated at around four million (Gould, 1974b). Here we observed the highest density of all species (43.27 birds/10 km²), eight times greater than sooties in the Line Islands (Table 2). Sooty terns are abundant year-round in the Phoenix Islands, with highest densities recorded from October to December (Gould, 1974b).

Their numbers at sea depend on their breeding cycles, which are often complex and unpredictable, even within a single island. In 1965, and from 1988 to 1990, Caroline Atoll had 19 colonies, each on a different cycle, giving rise to egg-laying in virtually every month (Clapp & Sibley, 1971a; Anne Falconer, personal communication; Kepler *et al.*, Subchapter 1.2, this vol.).

In Region III (Gilbert Islands) smaller numbers of sooty terns were observed (N = 113); we found moderate densities (4.00/10 km²), although the species is reported as uncommon at sea (Amerson, 1969). Our cruise track passed close to Aranuka, which is thought to harbor breeding colonies (Amerson, 1969).

In Region IV (Micronesia), we only observed sooty terns south of Kosrae and Pohnpei (N = 201); 200 of these were members of a single feeding flock. This species is known to breed in small numbers in Micronesia on Pohnpei, on several uninhabited atolls in the northern Marshalls (Baker, 1951; Amerson, 1969), and on Helen Reef (Engbring, 1983).

Although ranging entirely across the Pacific Ocean through southeast Asia into the Indian Ocean (Harrison, 1985), sooty terns have been seen only infrequently in the far western Pacific (Baker, 1951; Gould, 1974b). The POBSP found that the perimeter of their peripheral breeding localities is also the normal limit of their pelagic dispersal, and records beyond this have historically been attributable to climatic disturbances such as typhoons (Gould, 1974b).

Sooty terns, highly gregarious feeders and breeders, participated in 71.4% of all 14 feeding flocks and contributed 70.8% of all birds within the flocks (Tables 5.7; Fig. 7). Of 2,305 sooty terns observed, 1,467 (64%) were in feeding flocks, as was also found (65%) by Gould (1974b). Over our entire cruise track, only 4% were juveniles, suggesting that few sooty colonies had bred recently. By contrast, during March to May 1990 in the Line Islands, a much larger proportion of juveniles were observed (ICBP, 1990).

Crested Tern (*Thalasseus bergii*): We observed only two of these large, coastal, yellow-billed terns. Although a resident breeder on several island groups in the central and western Pacific and southeast Asia, it is everywhere uncommon (King, 1967; King & Dickinson, 1967; Amerson, 1969). Our birds appeared on the last day of the cruise as we entered Singapore Roadstead.

Brown or Common Noddy (*Anous stolidus*): This abundant tern breeds on almost all island groups in the Pacific, extending westward into southeast Asia (King, 1967; Pratt *et al.*, 1987). Although widespread, it generally occurs within 80 km of its breeding colonies. Much remains to be learned of the precise details of its dispersal patterns (Harrison, 1985).

The brown noddy was the third most abundant bird seen from the R/V *Akademik Korolev* (N = 259). An additional 203 noddies, seen in Micronesia, could not be identified to species. Since we saw no black noddies (*A. minutus*) in Micronesia, it is likely that they were also *A. stolidus*.

Although we sighted brown noddies in the Line, Phoenix, Gilbert, and Caroline Islands, we counted only five birds total. All well out to sea, some were 900 km from the nearest known breeding colony (ca. 7,700 birds at Phoenix Island, POBSP estimate, in Garnett, 1983).

Despite the fact that the Gilbert Islands are heavily populated, brown noddy densities were highest there (7.09 birds/10 km²): they were the most abundant bird in the region (Table 2). This species, which can nest in trees, is much more tolerant of humans than most seabirds. Pacific Ocean Biological Survey Program personnel also found that *A. stolidus* was common throughout the Gilberts up to 80 km from land (November to December, 1962 and 1964). It breeds on six islands in the southern Gilberts, including Abemama, near which we observed 235 brown noddies on 8 October.

In Micronesia, 18 brown noddies and 200 unidentified noddies (probably *A. stolidus*) close to Pohnpei probably originated on that island, where they are known to breed (Baker, 1951).

Brown noddies were regular members of feeding flocks, contributing 5% of their numbers (15% if the unidentified noddies are included) and participating in 36% of flocks (Tables 5,7). Corresponding figures from King (1970) are 7 and 11%.

Black or White-capped Noddy (*Anous minutus*): This species, smaller and darker than the brown noddy, breeds and disperses over the same range. It is more sedentary, however, and feeds closer inshore. Water temperature plays an important part in the pelagic distribution of both noddy species (Murphy, 1936): both are largely absent from cold-water upwellings.

Despite the black noddy's widespread distribution in the Pacific, we only observed six. Five were in the Line Islands within a few kilometers of Christmas Island, where approximately 10,000 breed (Garnett, 1983). The remaining bird was in the Gilbert Islands, where *A. minutus* may still breed. Twenty years ago there were small breeding colonies on eight islands (Amerson, 1969), including Maiana, which lay within 20 km of our cruise track.

Greatest densities (0.11 birds/10 km²) were within the Line Islands, where breeding populations exceed 40,000 (Stoddart, 1976). Colonies are smaller in the Phoenix Islands,

but it is surprising that we did not see one, as we passed within 80 km of Orona (Hull), where 10,000 birds have been reported (King, 1973). None participated in feeding flocks.

White or Fairy Tern (*Gygis alba*): Tolerant of man, the white tern breeds throughout the tropical Pacific. As with noddies, it is most common within 80 km of its breeding colonies, but may wander great distances out to sea (King, 1967; Pratt *et al.*, 1987).

The white tern was the fourth most common bird (Fig. 4) seen on the cruise (N = 146), occurring from the Line Islands to the Philippines. Many sightings were of ones and twos; the largest group (18) had been attracted to a large feeding flock south of Pohnpei, Caroline Islands.

At-sea densities of white terns, as for many other tropical species, reflect in part their breeding phenology, especially for the more remote islands. Line Islands densities were low (0.05 birds/10 km²) in September 1988 but much higher in March to May 1990 (ICBP, 1990). Perry (1980) estimated 17,050 white terns in the Line Islands and noted that they ranged widely and bred all year. Densities in the Phoenix Islands were higher (0.31/10 km²), a surprise considering that the overall population (10,000 birds; Clapp, 1967) is smaller.

White tern densities were greatest (2.01 birds/10 km²) in the Gilbert Islands, due in large part to 89 birds seen the day before anchoring at Tarawa. In Micronesia, 36 *G. alba* were observed south of Kosrae and Pohnpei, and one was found north of Ulithi Atoll. Baker (1951) implies that it is common in Micronesia, especially on low islands: Ulithi is listed as a breeding site.

White terns are not listed for the Philippines (Delacour & Mayr, 1946; King & Dickinson, 1975). The species evidently rapidly decreases in density west of Micronesia. Our most westerly sighting, an adult flying southwest at 11°00'N, 132°59'E was approximately 480 km north-northwest of Belau, the closest landfall, and on the extreme western Pacific limit of the white tern's known range. This is the maximum distance that we observed this species from land.

Feeding Flocks

A seabird feeding flock is regarded as an association of five or more individuals acting as a unit (Gould, 1974b). In this study we encountered both monospecific and mixed-species flocks. We did not see any large associations of seabirds that were not feeding flocks (i.e., flocks of direct migrants). The following analysis deals with the size, abundance, composition (species and family), and geographic distribution of the 14 feeding flocks we encountered.

Flock Size and Abundance

Flock sizes ranged from 8 to 420 birds, averaging 148 birds per flock. The total number of birds in feeding flocks (N = 2,070) represented 56.5% of our bird sightings, a figure comparable to the 69.5% found in 893 flocks by POBSP (King, 1970).

The smallest flock (N = 8), of seven white terns and one brown noddy, occurred in the Gilbert Islands on 8 October. The largest flock (3 October in the Phoenix Islands) was monospecific (420 sooty terns). The second largest (N = 408)

contained 7 species and was predominantly composed of wedge-tailed shearwaters (86%) and unidentified noddies. It was encountered on 13 October adjacent to Pohnpei. Three environmental factors undoubtedly contributed to the size and diversity of this flock:

1. The flock was near a high island at 07°N, within the Equatorial Countercurrent boundaries (ca. 4°N and 9°N), where particularly rich upwellings provide feeding grounds for both fish and birds (Ashmole & Ashmole, 1967; Gould, 1974a);
2. Flying fish, considerably more abundant compared to the previous 3 days, indicated increased productivity; and
3. The flock was attracted to masses of predatory fish (primarily tunas) vigorously leaping from the water, causing the water to "boil."

Flock Composition

Five families (Laridae, Procellariidae, Fregatidae, Sulidae, Phaethontidae), 12 species, and 3 unidentifiable group categories were represented in feeding flocks. Sooty terns dominated the feeding flocks, followed numerically by noddies and wedge-tailed shearwaters (Fig. 7; Tables 5, 7). These three species groups accounted for 95% of all birds seen in flocks.

Sooty terns participated in 71.4% of all flocks (Table 7), a similar proportion to that found by POBSP (76.0%) over a longer time frame (King, 1970). White terns were found in 57% of the flocks, noddies (primarily brown noddy) in 38%, and wedge-tailed shearwaters in 29%.

White terns were also regular, though minor, members of pelagic feeding flocks, found in 57% of all flocks and representing 2% of total numbers (Table 7, Fig. 7). King (1970) found that white terns participated in 9% of flocks and noted that the relatively high flocking tendency of white terns

was of interest since this species had been thought to be a solitary feeder. Our data also suggest that the white tern commonly joins mixed-species feeding flocks.

White terns are generally more solitary on land and at sea and have not been found to exhibit such a high rate of flock participation (57.1%) as we observed (King, 1970). This species, however, joined flocks only in small numbers. Overall, five white terns on our cruise joined over half the flocks, but their total numbers within flocks accounted for only 2.1% (Fig. 7; Table 7).

Geographic Distribution

We encountered feeding flocks in Regions I through IV (Table 5), viz., in the Pacific Ocean from 150°W to 158°E longitude. We saw no flocks from Pohnpei westward to Singapore.

We found only one flock, composed of 85 sooty terns, in the Line Islands. More than half the flocking birds were within the Phoenix Islands (Table 5), where the highest seabird populations and greatest species diversity were found. Great frigatebirds joined flocks only in the Phoenix Islands.

In Region III (Gilbert Islands), sooty terns, brown noddies, and white terns were the only species present in feeding flocks. Sooty terns and brown noddies accounted for 92% of flocking birds in this area (Table 5).

Region IV (Micronesia) was relatively rich in feeding flocks that contained several species not encountered elsewhere: stercorariids, Kermadec and Bulwer's petrel, Audubon's shearwaters, and white-tailed tropicbirds.

The feeding flocks we observed were found in areas known to be nutrient-rich. In broad terms, latitudes north of 10°N and south of 10°S are poor in nutrients. The zone in-between, especially from 04 or 05°N to 09 or 10°N (Equatorial Countercurrent) and from 00 to 09 or 10°S, is considerably richer in plankton and schools of small fish and tuna (Ashmole & Ashmole, 1967). Superimposed on this general pattern are local upwellings of plankton or "fronts" that occur close to islands and are particularly evident between 01°30'S and 05°N (King & Hida, 1957).

The geographic distribution of our feeding flocks fits these general patterns (Fig. 8). Their latitudinal limits were 07°N and 07°S. At 02°S, within the plankton bloom on either side of the equator, we encountered a feeding flock of 153 birds. Flocks were more frequent around island clusters. We saw four flocks each close to the Phoenix and Gilbert Groups, and the day our ship arrived at 05°N (13 October, south of Pohnpei) we immediately observed a substantial increase in flying fish. From 04°N to 07°N, we encountered 3 feeding flocks of 223, 22, and 408 birds, respectively. The dearth of fish, and, hence, seabirds, north of 10°N was particularly evident. Not only were there no feeding flocks, there was a substantial decrease in the number of birds compared to all other Pacific areas (Table 1).

We saw no flocks in southeast Asia, where total numbers of birds were low. Here we encountered complicating factors due to heavy pressures from commercial and subsistence fisheries and other human population factors, which override changes in oceanography that are associated with the continental

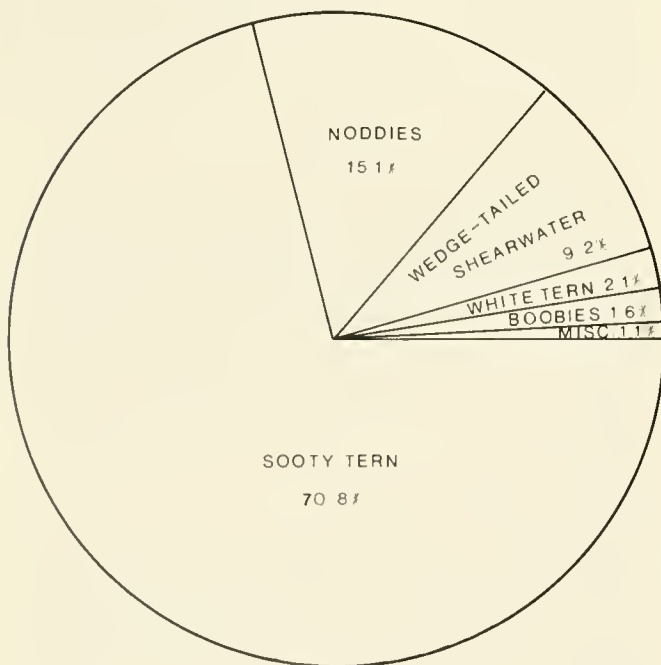


Fig. 7. Relative abundance of species or species groups found in all feeding flocks (N = 14). Total number of birds was 2,072 (\bar{x} = 148).

shelf. Southeast Asia has long been recognized as an outstanding area for fish and, until the last few decades, was similarly rich in seabird colonies (Nelson, 1978).

Regional Discussions

Region I (457 birds, 26 species, 7 families)

Region I (Fig. 1) begins with the waters between the Line Islands and Hawaii north to 14°N. The Line Islands are a scattered group of five atolls, five islands, and two submerged reefs straddling the equator between 06°N and 12°S latitude, and 162° and 150°W longitude. They are all low islands with extremely varied ecology ranging from barren, tropical deserts with scarcely any vascular plants to lush forests of coconut palms and/or indigenous vegetation.

All except three are uninhabited and thereby serve as suitable habitats for tropical seabirds. Together with the Phoenix Islands, they constitute the largest assemblages of breeding tropical seabirds in the Pacific, both in species diversity and abundance. Christmas Island, with 18 species of breeding seabirds, is one of the richest seabird islands in the world (Ashmole & Ashmole, 1967; Garnett, 1983), due in part to equatorial upwellings and plankton associated with the seasonal movements of the North and South Equatorial Currents and Countercurrents (King & Hida, 1957; Ashmole & Ashmole, 1967).

Overall, we found greater seabird diversity and density in the Line and Phoenix Islands (Tables 1,2,4). Two major groups of birds were most abundant in Region I: shearwaters/petrels and terns. Of minor importance numerically were boobies and storm-petrels (Table 3). Of interest is the high proportion of resident breeders and wintering birds (Fig. 3).

The 1982–1983 anomalous warm waters associated with the El Niño Southern Oscillation severely disrupted seabird breeding on Christmas Island (Schreiber & Schreiber, 1984). Furthermore, feral cats, developmental threats, and increased poaching associated with expanding human populations are ongoing problems on Christmas, and these affect the numbers of birds seen at-sea in the area (Gilbert and Ellice Islands Gov., 1974; Garnett, 1983; Teeb'aki, personal communication).

In the Line Islands, we extended the known range of herald petrel and added sightings of Cook's petrel (six) and Stejneger's petrel (two), both rarely recorded in the area.

Region II (1,796 birds, 24 species, 6 families)

The Phoenix Islands (Fig. 1) form a relatively compact group of eight low islands lying from 03° to 05°S. Most are dry and waterless. All except Canton are uninhabited and harbor, like the Line Islands, some of the richest and largest seabird colonies in the world. They lie within the boundaries of the South Equatorial Current (04°N to ca. 10°S), a region rich in plankton and associated fish schools (King & Hida, 1957; Ashmole & Ashmole, 1967).

At-sea bird observations were dominated by sooty terns (96% of total), with procellariids next in abundance (Table 3). Small numbers of frigatebirds, boobies, and storm-petrels occurred, as in Region I (Table 2). Resident breeders, nonbreeding visitors and direct migrants were all well-represented (Fig. 4). The highest density of any bird on this cruise was in this area—sooty terns, at 32.45/10 km².

In the Phoenix Islands we recorded a range extension of the little shearwater, and added three sight records of Cook's petrel, and nine of wedge-tailed shearwaters (Table 6). Because of the remoteness and unsuitability of the Phoenix Islands for

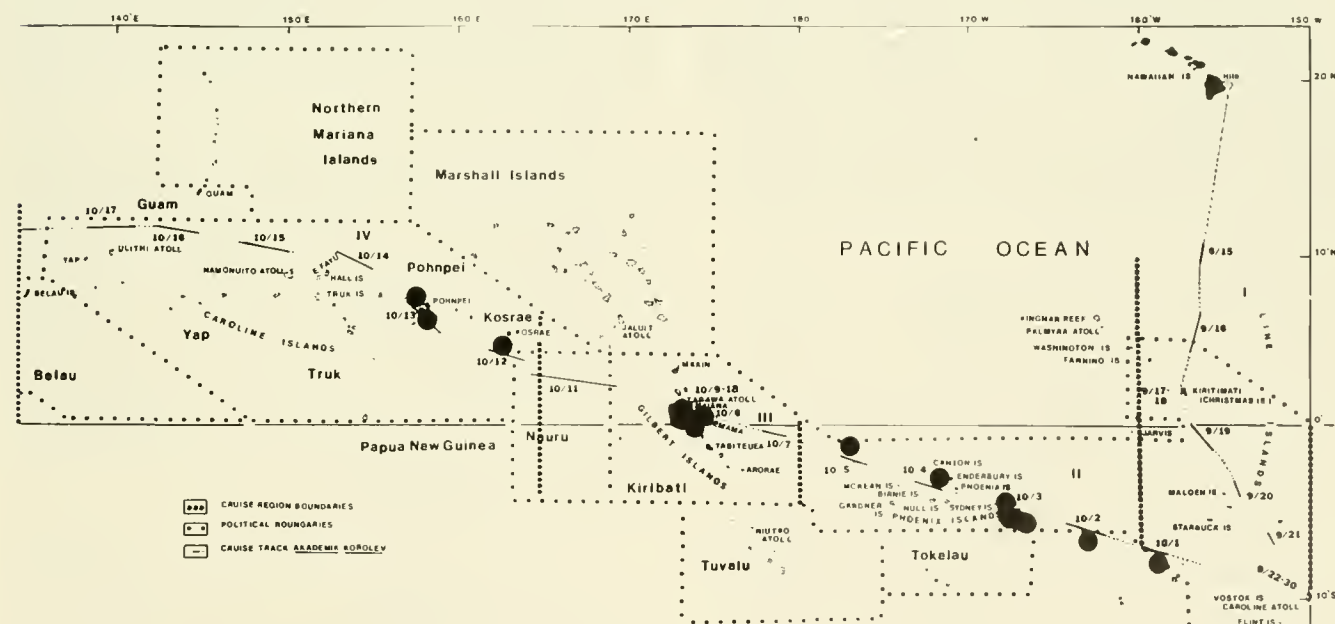


Fig. 8. Geographic distribution of feeding flocks (dots).

human settlement (Howland and Baker are US National Wildlife Refuges, and Birnie, McKean, and Phoenix Islands are Kiribati Wildlife Refuges), its seabirds appear reasonably safe from disturbance for the present.

Region III (495 birds, 13 species, 5 families)

The Gilbert Islands (Fig. 1) stretch in a compact arc from 03°17'N to 02°38'S latitude and from 176°49'E to 172°48'E longitude. They compose a single archipelago of 11 atolls and 5 reef islands, forming a southerly extension of the Marshall Islands.

All the Gilbert Islands are populated, some heavily. Since the 1-Kiribati have long utilized seabirds and their eggs for food, species sensitive to human disturbance (shearwaters, petrels, boobies, tropicbirds) are absent. The primary breeding species are tree-nesters such as brown noddies and white terns (Table 4).

Our observations were dominated by larids (Table 3). Brown noddies (48%) and sooty terns (27%) composed 92% of flocking birds. With the exception of a few boobies, most other birds were nonbreeding visitors (Table 4). Migrants were absent (Fig. 3). We also provide additional sightings of such rarities in the region as Cook's petrel (1), Kermadec petrel (2), south polar skua (5), and wedge-tailed shearwater (213) (Table 6).

Region IV (799 birds, 18 species, 10 families)

Our cruise track passed south of the districts of Kosrae and Pohnpei, then north of Truk, Yap, and Belau (04°N to 10°N latitude, 163°E to 138°E longitude). Micronesia contains fewer people on far more islands than the Gilberts. However, fishing fleets from several foreign countries are exploiting their oceanic waters, and the presence of even a few people on an islet deters many seabird species from successful breeding.

Our observations from the Caroline Islands were dominated by sooty terns and noddies (52% of birds seen), but procellariids and boobies were represented in fair numbers. Skuas first appeared here, along with the only migrant duck. The wedge-tailed shearwater attained a density of 2.93 birds/10 km² (Table 2). Our observations of brown boobies suggest the possible existence of a colony on Magur Islet, Namonuito Atoll, in the District of Truk.

Region V (34 birds, 6 species, 4 families)

The Philippine Sea and Basin (Fig. 2) exhibited the lowest biodiversity and species densities (Tables 1–4) of the five Pacific regions. This relatively small area, little-known ornithologically and with no islands for hundreds of kilometers, stretches west of the Marianas to the Philippines (at 11°N latitude, from 136°E to 125°E longitude). The nearest landfalls are the Marianas to the northwest, Belau, New Guinea, and the Moluccas (Indonesia) to the south, and the Philippines to the west. Plankton productivity and fish populations are known to be considerably poorer in tropical waters north of 09°N than further south (Ashmole & Ashmole, 1967). Our sightings of six streaked shearwaters suggest that the southerly migration corridor for this species lies entirely east of the Philippines.

Region VI (22 birds, 4 species, 6 families)

The Bohol (Mindanao) and Sulu Seas stretch from 125°E to 117°E. Seabird densities were low. Phalaropes, not previously encountered on our cruise, accounted for over half the total bird count (Table 3). A few larids, skuas, brown noddies, and wedge-tailed shearwaters (our most western observations) completed the list. The proportions of resident breeders, nonbreeding visitors, and direct migrants were equal (Fig. 4). Elevated human populations in the Philippines have undoubtedly reduced seabird numbers.

Region VII (65 birds, 8 species, 5 families)

Our cruise track passed through the South China Sea between 07°N to 01°N latitude and 117°E to 104°E longitude. The route passed from the Balabac Strait (southwestern Philippine Islands) indirectly to Singapore (Fig. 2). These waters, the most heavily polluted of the trip (see Chapter 2, this vol.), are heavily fished commercially, and human population densities around their periphery are high. Seabirds were sparse. As with Region VI, phalaropes contributed half of the total. Migrant stercorariids formed the next most common bird grouping; since stercorariid records are few from this area, our observations of 12 birds of at least 2 species add to their known dispersal areas.

Gulls and terns were in surprisingly few numbers, considering that almost 20 species occur in the South China Sea. We recorded Caspian, bridled, and crested terns (and a few unidentified larids) in very small numbers. Resident breeders and nonbreeding visitors numbered only one species each, and there were four species of migrants (Fig. 3).

During our indirect, 9-day passage across the South China Sea (23–31 October) we encountered approximately 150 land birds (including 40 raptors), totaling at least 20 species (Ellis *et al.*, 1990 and Subchapter 3.6, this vol.). The presence of owls, nightjars, falcons, a large crane, and small forest birds provided a highly interesting replacement for the expected terns, gulls, and other seabirds.

This area is little known ornithologically, at least in English publications (Delacour & Mayr, 1946; Delacour, 1947; Anon., 1975; Jing-Xiam & Zi-Yu, 1975; Nelson, 1978; Hails, 1987; King & Dickinson, 1987). We added three parasitic jaegers to records for the South China Sea and a possible range extension of the masked booby. Unfortunately, in the last few decades numerous large seabird colonies in this area have been destroyed by direct human predation (Nelson, 1978) but considerable efforts towards conservation of islands, reefs, bays, and varied habitats are on-going commitments by all countries concerned, assisted by international agencies (UNEP, 1984a,b; IUCN, 1988a,b).

This First US-USSR Central Pacific Expedition resulted from the efforts of many people in the United States and the Soviet Union. On the American side, the primary organization and financial support were from the US Fish & Wildlife Service. We especially appreciate the efforts of Harold J. O'Connor, Director, Patuxent Wildlife Research Center and Steve Kohl (Office of International Affairs). We thank H. Randolph Perry for suggesting and encouraging our participation in the expedition, Paul Sykes for willingly assuming the Michigan

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3.6 Evidence for a Major Fall Land Bird Migration Corridor Across the South China Sea from Indo-China to the Greater Sunda Islands

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Introduction

Until 1960, bird migration corridors in eastern Asia were poorly known (Wetmore, 1926; Delacour, 1947; McClure, 1974; Medway & Wells, 1976). In southeast Asia, however, the geography of the land masses surrounding the South China Sea seems to create natural funnels that should concentrate migrant land birds into three primary fall corridors. Important flight paths along some of these routes have recently been discovered.

It is known that migrants from Japan and eastern China island-hop south through the Philippines (Wetmore, 1926; McClure, 1974), with Ng (1978) presenting evidence that barn swallows (*Hirundo rustica*) move directly from mainland China to the Philippines. McClure (1974) asserted that many migrants passing through the Philippines to Borneo fly west from Palawan, then south to Borneo. Simpson (1983a,b) encountered hundreds of migrant birds at the Tembungo offshore oil drilling platform near the northeastern tip of Borneo (Fig. 1) during the fall migration of 1981. Although he reported these observations as evidence of a passage directly across the South China Sea, his location near Balabac Strait also suggests that these migrants could have been moving south from the Philippines.

Geography suggests that many migrant land birds in Burma and western Thailand would move south along the Malay Peninsula, a pathway known to be important (McClure, 1974; Medway & Wells, 1976; Hails, 1987), and thence across the narrow Straits of Malacca to Sumatra. However, migrants from east Thailand as well as those from China, Laos, and

Vietnam, moving down the Indo-China Peninsula would naturally converge south of the Mekong River Delta on Mui Bai Bung. From this tip of the Indo-China Peninsula, birds traveling overland must fly northwest into Thailand before proceeding south. Those capable of a relatively short (ca. 400 km) overwater flight can fly southwest across the Gulf of Thailand toward the Malay Peninsula, a route portrayed by McClure (1974) and Hails (1987) as a minor pathway for the migrants from Indo-China.

McClure (1968, in McClure, 1974) illustrated a coastal migration route from Taiwan to northern Vietnam, thence south, crossing the South China Sea to Borneo, another route suggested by geography. However, he provides scant evidence for such a corridor and no evidence that migrants are concentrated at Mui Bai Bung. McClure (1974) discussed a fall passage of willow warblers (*Phylloscopus* sp.) across the South China Sea to Sarawak without offering details on their point of origin north of the sea. Simpson (Wells, personal communication and in prep.) reported a substantial fall movement of land birds (36 species) in the Terengganu oil field (ca. 05°25'N, 105°13'E, see Fig. 1). Although this location is only about 200 km east of the Malay Peninsula and west of a direct route to Borneo, Simpson's records provide the best evidence to date of a direct South China Sea crossing. The birds observed by Simpson (1983a) at the Tembungo oil terminal could have come from Vietnam, as he suggests, but the source of these migrants is clouded by their proximity to the Philippines. Although biologists from the Chinese Academy of Science and the Beijing Natural History Museum (Anon., 1974) noted 44 species of land birds during 1974 surveys of islets in the



Fig. 1. Geography of the southern half of the South China Sea showing bird survey locations. Numbered segments are bird location survey locations for R/V *Akademik Korolev*, 23–31 October 1988.

northern two-thirds of the South China Sea, demonstrating the potential for long-distance (ca. 1,000 km) migration, they did not demonstrate that a corridor for land-bird migrants exists further south between Vietnam and Borneo. In this paper, we present data from the South China Sea that strongly support the presence of such a migration route.

Study Area and Methods

We encountered migrant land birds during our 23–31 October 1988 indirect passage (Fig. 1) from Balabac Strait to Singapore on the Soviet research vessel *Akademik Korolev*. While in transit, we observed birds during dawn-to-dusk seabird surveys from the flying bridge (12 m above sea level). During a 3-day period while the ship was anchored or drifting without power to conduct oceanographic research (Fig. 1, Station 13; 06°01'N, 106°55'E), we conducted periodic walking inspections of the ship (usually at half-hour intervals) and searched the ship each night by flashlight to count roosting birds. Five raptors and several barn swallows were captured by hand (primarily at night) and examined for physical condition.

Results and Discussion

During our 9-day passage, we encountered about 150 land birds (121 by conservative count, 84 minimum count, Table 1) representing 14 families. Almost all were migrants that winter (at least in part) south of the South China Sea. Most of these birds (96 by conservative count) arrived on the ship during the 3-day period while we were stationary (Fig. 1, Station 13) around 350 km southeast of the southern tip of Indo-China. The presence of land birds at this location suggests that they were in passage across the South China Sea from Indo-China to the Greater Sunda Islands. The low bird counts seen before

arriving at and after leaving this location (Table 2) suggest that this spot lies on a rather narrow migratory pathway although, alternately, birds may have been reluctant to approach a moving vessel. Simpson's 1982 observations (Wells, in prep.), made in the Terengganu oil field (Fig. 1) very near our cruise track, suggested that he was sampling the same corridor we visited; if so, the pathway may be somewhat wider than we detected.

The number of birds we observed (Tables 1,2) is small when compared with record counts for well-known migration pathways. However, our visit was brief and probably too late for detecting the bulk of migrating land birds. Simpson's (1983a) dates for six of nine frequently encountered land birds near northeastern Borneo fell before the time of our visit, and, just as important, migrating land birds most often aggregate where land and water configurations encourage them to collect (e.g., on north or south projecting peninsulas). By contrast, we were on the open sea where birds are much less likely to concentrate. Considering these factors, it seems likely that adequate spatial and temporal sampling will reveal many thousands of land birds moving south from Indo-China across the South China Sea.

Although our records and those of Simpson's (Wells, in prep.) demonstrate that a sizable migration is probably normal across the South China Sea, we should mention an alternate hypothesis that may help explain the presence of these birds where and when we observed them. First, our passage occurred when Typhoon Ruby was ravaging the Philippine Islands (Anon., 1989). Although we did not encounter heavy seas or strong winds, some of the birds we observed may have been forced out to sea, if nonmigratory, or shunted away from their normal migration route, if migratory, by the storm. However, most of the birds we observed far from land (Table 3) are known to be strong migrants. The four hawks tentatively identified as shikras (*Accipiter badius*) and crested goshawks (*A. trivirgatus*), and the dove (*Streptopelia* sp.) are the only real surprises, although a few others in Table 3 would not be expected this far from land.

Flight direction may give some indication of the likelihood of either hypothesis. If the birds were displaced migrants, they would probably have been heading southwest (i.e., away from the storm). If in passage from a concentration zone on the Indo-China Peninsula to Borneo, they should have been heading southeast to encounter our vessel. If, as we observed, the raptors (33% of all land birds) were foraging at sea (Ellis *et al.*, 1990) rather than migrating, there would likely be no consistent trend in their flight direction. In Fig. 2, there is no clear east-west trend in arriving or departing flights. However, although the data are very few, strong southward and westward components are evident. In constructing Fig. 2, we eliminated directional readings for birds seen on cruise track segments 1–7 and 20–30 because these segments were near enough to land (i.e., within 100 km) that the birds' flight directions could have been influenced by sight or sign of nearby land. In addition, all flight bearings could have been influenced by the presence of the ship.

Physical condition of the birds we observed may also be an indicator of the regularity with which this migration route is used. If a high proportion of the known overseas migrants were

TABLE 1

Land bird totals for R/V *Akademik Korolev* cruise track segments and stationary watches in the South China Sea, October 1988.

Date	Station/ Number	Segment ² Length (km)	Duration of Obs. (min.)	No. Land Birds Observed ¹					
				Raptors		Non-raptors		All Land Birds	
				Min.	Cons.	Min.	Cons.	Min.	Cons.
23	1	38	88	0	0	0	0	0	0
	2	15	45	0	0	0	0	0	0
24	3	6	17	0	0	0	0	0	0
	4	67	158	0	0	0	0	0	0
	5	14	44	0	0	0	0	0	0
	6	19	48	0	0	0	0	0	0
	7	49	109	0	0	1	1	1	1
25	8	22	50	0	0	0	0	0	0
	9	3	11	0	0	0	0	0	0
	10	30	67	0	0	0	0	0	0
	11	17	38	0	0	0	0	0	0
	12	63	143	0	0	4	4	4	4
26-28	13	ca. 0	912	22	30	32	44	54	74
28	14	ca. 0	43	1	1	0	0	1	1
	15	22	10	0	0	0	0	0	0
	16	26	78	0	0	0	0	0	0
	17	ca. 0	195	1	4	4	8	5	12
29	18	ca. 0	105	1	1	1	4	2	5
	19	ca. 0	20	0	0	0	0	0	0
	20	25	62	0	0	0	1	0	1
	21	ca. 0	80	0	0	0	0	0	0
30	22	ca. 0	23	1	1	3	3	4	4
	23	ca. 0	110	0	0	2	4	2	4
	24	ca. 0	25	0	0	0	1	0	1
	25	ca. 0	95	0	1	3	3	3	4
	26	ca. 0	54	0	0	0	0	0	0
	27	ca. 0	52	0	0	3	5	3	5
	28	ca. 0	30	1	1	0	0	1	1
31	28	ca. 0	15	0	0	0	0	0	0
	29	ca. 0	15	0	0	0	0	0	0
	30	135	280	1	1	3	3	4	4
TOTALS			3,022	28	40	56	81	84	121

¹ Because accurate bird counts were sometimes difficult to obtain for stationary watches (i.e., some birds remained aboard or flew about the ship for extended periods), we report both the minimum (min.) number of birds observed (based on subtractive values) and a conservative (cons.) number based primarily on new arrivals. The actual number observed is believed to be about 20% higher than the conservative count.

² Cruise track segment locations are illustrated in Fig. 1.

TABLE 2

Minimum and conservative land bird counts along cruise track of R/V *Akademik Korolev* in the South China Sea, 23–31 October 1988.^{1,2}

Species	Segments 1–7 (Oct. 23–24)		Segments 8–19 (Oct. 25–29)		Segments 20–30 (Oct. 29–31)	
	Min.	Cons.	Min.	Cons.	Min.	Cons.
Small juv. accipiter (<i>Accipiter</i> sp.)	0	0	14	24	3	3
Ad. Japanese sparrow-hawk (<i>Accipiter gularis</i>)	0	0	2	2	0	0
Ad. shikra (<i>A. badius</i>) ³	0	0	1	2	0	0
Ad. crested goshawk (<i>A. trivirgatus</i>) ³	0	0	2	2	0	0
Eagle/kite (Accipitridae)	0	0	1	1	0	0
Peregrine falcon (<i>Falco peregrinus</i>)	0	0	3	3	0	0
Oriental scops owl (<i>Otus sumia</i>) ⁴	0	0	2	2	0	1
Chinese pond heron (<i>Ardeola bacchus</i>)	0	0	0	0	3	3
Watercock (<i>Gallicrex cinerea</i>)	0	0	1	1	0	0
Dove (<i>Streptopelia</i> sp.) ³	0	0	1	1	0	0
Grey nightjar (<i>Caprimulgus indicus</i>)	0	0	1	1	1	1
Fork-tailed swift (<i>Apus pacificus</i>)	0	0	4	4	0	0
Swift (Apodidae)	0	0	2	2	0	0
Dollarbird (<i>Eurystomus orientalis</i>)	1	1	0	0	0	0
Barn swallow (<i>Hirundo rustica</i>)	0	0	14	29	5	10
Swallow (<i>Hirundo</i> sp.)	0	0	1	1	0	0
Ashy minivet (<i>Pericrocotus divaricatus</i>) ⁴	0	0	1	1	1	1
Lanceolated Warbler (<i>Locustella lanceolata</i>) ⁴	0	0	1	1	1	1
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	0	0	1	1	0	0
Warbler (<i>Acrocephalus</i> sp.)	0	0	1	2	1	1
Arctic warbler (<i>Phylloscopus borealis</i>)	0	0	0	0	1	1
Flycatcher (<i>Ficedula</i> sp.)	0	0	2	2	0	0
Brown shrike (<i>Lanius cristatus</i>)	0	0	6	6	1	1
Unidentified passerines or remains	0	0	5	8	0	1
TOTALS	1	1	66	96	17	24

¹Cruise track segments and stations are illustrated in Fig. 1 and described in Table 1.

²Abbreviations in column headings are: Min. (minimum count) and Cons. (conservative count) as explained in Table 1, Footnote 1.

³Because these birds are considered non-migratory, these identifications should be treated as tentative. All are based on nearby visual observations aided by 10x binoculars, but without photographic or other substantiation.

⁴Individuals of these species were deposited in the US National Museum: Oriental scops owl, USNM No. 607190; Ashy minivet, USNM No. 607193; and Lanceolated warbler, spirit specimen (not assigned numbers at USNM).

in good body condition this far from land, it is more tenable to suppose that these species regularly use this route. In Table 3, our best estimate of physical condition is compared for all species that we encountered far from land. We know from handling a few captives, and infer from the energetic flight of others, that the raptors and the barn swallows at Station 13 (Fig. 1) were in good physical condition. For the other species, too few individuals were present to draw firm conclusions, but all birds of most species appeared to be in good condition.

A final hypothesis may explain the presence of some of the raptors. Many were opportunistically foraging at sea. During our 3-day layover (Fig. 1, Station 13), we recorded raptors perching for extended periods, roosting nightly on the ship, and

engaging in at least 21 hunting forays (Ellis *et al.*, 1990). Of 14 forays for which the outcome was known, 13 (93%) were successful. Some accipiters even used the ship's deck lights to forage at night. We gathered prey remains, totaling at least 20 kills. Two species, barn swallow and brown shrike (*Lanius cristatus*), suffered heavy mortality from predation. Of 14 barn swallows (minimum count) observed from 25–29 October, at least 7 turned up as prey. Even more significant, five of six (minimum count) brown shrikes seen during the same 5-day period were observed as prey. Simpson's (1983a; Wells, in prep.) observations of raptor behavior at both oil fields led him to conclude that Japanese sparrow-hawks were hunting and "commuting between nearby rigs." Our observations confirm

TABLE 3

Physical condition and migratory status of land birds arriving on R/V *Akademik Korolev*, 25–29 October 1988, South China Sea.¹

Physical Condition ³	Taxon [Number]	Mobility Classes ²				Comments
		Known Migrant	Known Over-water Migrant ⁵	Known Colonizer of Islands	Known Straggler to Islands	
Good	Japanese sparrow-hawk (<i>Accipiter gularis</i>) [2]	+	-	-	-	Common migrant
Good	Shikra (<i>A. badius</i>) [2]	+	-	-	-	Western population is highly migratory; eastern population migratory in Malaysia
Good	Crested goshawk (<i>A. trivirgatus</i>) [2]	-	-	-	-	Non-migrant throughout range
Good	Peregrine falcon (<i>Falco peregrinus</i>) [3]	+	+	+	+	
Fatigued	Watercock (<i>Gallicrex cinerea</i>) [1]	+	-	-	-	Winters in Greater Sunda Islands and Celebes; very few records as straggler
Good	Dove (<i>Streptopelia</i> sp.) [1]	-	-	-	-	
Emaciated	Oriental scops owl (<i>Otus sunia</i>) [1]	+	-	-	-	
Good	Gray nightjar (<i>Caprimulgus indicus</i>) [1]	+	+	-	+	Strongly migratory, scatters across Malaysia in winter
Good	Fork-tailed swift (<i>Apus pacificus</i>) [4]	+	-	-	-	A few migratory stragglers recorded as far east as Marshall Islands
Good	Barn swallow (<i>Hirundo rustica</i>) [29]	+	+	-	+	Winters throughout region and tropics worldwide
Fatigued	Ashy minivet (<i>Pericrocotus divaricatus</i>) [1]	+	-	-	-	Winters on larger islands of Indonesia, but not on islands separated by large bodies of water
Fatigued	Lanceolated warbler (<i>Locustella lanceolata</i>) [1]	+	-	-	-	Winters in Greater Sunda Islands
Good	Great reed warbler (<i>Acrocephalus arundinaceus</i>) [1]	+	+	-	+	Common migrant in Indonesia
Good	Brown shrike (<i>Lanius cristatus</i>) [6]	+	+	-	-	Common migrant to Greater Sunda Islands; recorded in Palau

¹Data are included only for that portion of the cruise track (stations 8–19) where the ship was far (>100 km) from land.²Symbols in these columns: + = yes, - = no. Assignment to mobility class (i.e., regular migrant over land and over large bodies of water >500 km, colonizer of distant land masses and islands as a breeding bird, straggler either on migration or as a resident) is at best tentative for some species, but was derived from information in Brown & Amadon (1968), Clements (1978), King & Dickinson (1975), Medway & Wells (1976), and Pratt *et al.* (1987).³Physical condition was reported “Good” if bird flew well and was adept at avoiding capture by hand, “Fatigued” if readily captured by hand, and “Emaciated” if sternum was sharply protruding upon capture.

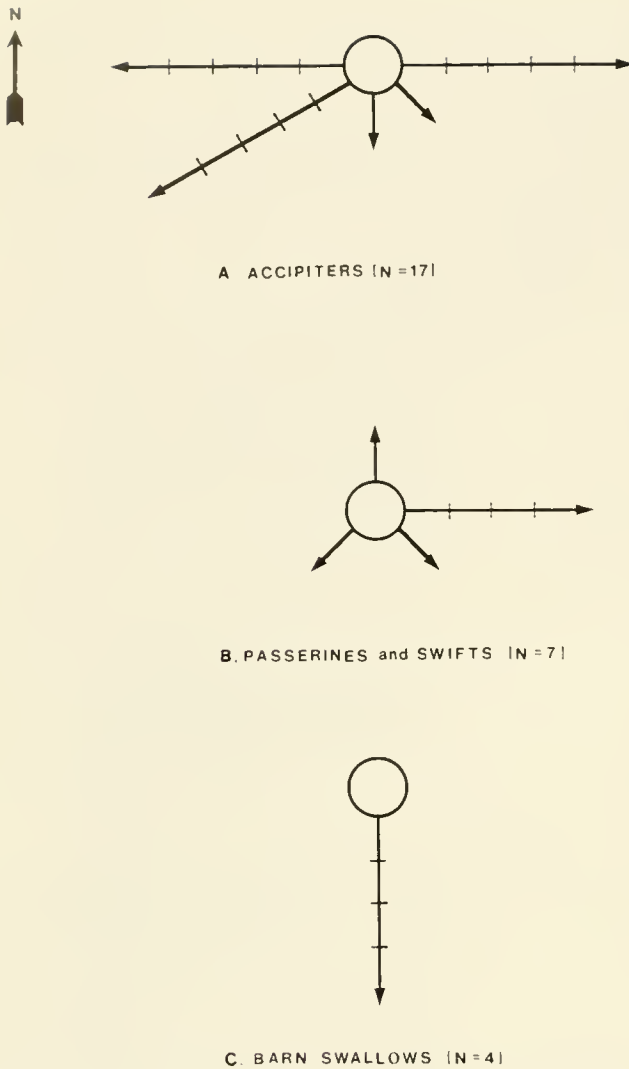


Fig. 2. Arriving and departing flight directions for birds seen on cruise track segments 8-19 of R/V *Akademik Korolev*, 26-29 October 1988.

that the raptors were opportunistically using our stationary ship for perching, roosting, hunting, and eating. When the ship was moving under power, however, none of the raptors perched for any extended period, and none roosted on the ship.

From all available evidence, it seems most likely that the birds we encountered were a small part of what must be a sizable wave of fall migrants on their way across the South China Sea. The configuration of the land masses suggests that the point of departure for these birds was the southern tip of Indo-China; however, further land-based research is needed to substantiate the point of origin and destination of birds crossing the South China Sea to Borneo. Additional work at sea will also be helpful in determining the timing and magnitude of the migration, as well as corridor width. Work on islands in the South China Sea or stationary platforms may substitute in part for the at-sea studies, but it is also important to determine body condition of birds arriving in the Greater Sunda Islands. Intensive banding operations in Vietnam, at sea, and in Borneo could reveal much about survival rates and all other aspects of this little-known migration route.

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General Conclusions

The BERPAC expedition of 1988 instituted a series of research projects that greatly amplified the scope of the original program's overall research objectives. The cruise included an 8-day stay on Caroline Atoll, an uninhabited necklace of islets enclosing a pristine lagoon. Chapter 1 deals at length with the history, geology, reef structure, botany, and ornithology of this little-studied ecosystem. Notable features of the atoll included a nearly-continuous reef surmounted by 39 islets in various stages of plant succession, many of them covered in virgin forest (Subchapter 1.1); a community of 11 species of breeding seabirds, numbering in excess of 1,000,000 individuals (Subchapter 1.2); and a remarkable *Acropora*–*Tridacna* reef containing the world's densest known colony of *Tridacna* clams (Subchapter 1.4). The inner reef system has developed within a lagoon that is perched several inches above sea level at low tide. New species of plants, lizards, land birds (Subchapter 1.3), and seabirds were discovered for the atoll during the 1988 expedition.

Caroline also provided an opportunity to compare basic oceanographic parameters between the open ocean, an enclosed lagoon, and the confined waters of the South China Sea.

In Chapter 2, one of the more recent aspects of marine pollution—plastic contaminants—was examined in the central Pacific Ocean and South China Sea. Surface and subsurface water was sampled and the quantity and distribution of plastic debris determined. Plastics collected from the water were extracted and analyzed for organic pollutants to assess the potential hazard of the transfer of pollutants to marine organisms that ingest plastics. Results of sampling revealed that plastic debris, and specifically raw polyethylene pellets used in manufacturing, is widespread in the Pacific Ocean and South China Sea. Plastics occurred more frequently than did tar balls,

even in the South China Sea. Organic contaminants were not associated with plastics at any detectable levels. However, subsequent studies demonstrated that plastics can adsorb certain contaminants and that this could represent a potential hazard to marine life.

In Chapter 3, primary productivity was compared between waters close to and distant from Caroline Atoll. Waters close to Caroline showed less productivity than waters nearer to the equator (Subchapters 3.1 and 3.2). Not surprisingly, mesozooplankton (Subchapter 3.3) and neuston (Subchapter 3.4) diversity and biomass also increased toward the equator, relative to the waters near Caroline, due in part to the hydrodynamics of the water columns near the equator. The equatorial parts of the Pacific were also much richer in seabird diversity and density than waters at higher latitudes (Subchapter 3.5). One surprise of the expedition was the discovery of a major land bird migration corridor over the South China Sea from Vietnam to Borneo (Subchapter 3.6).

The second leg of the 1988 BERPAC expedition was the first of a planned series of similar cruises in the tropical Pacific and, as such, should be viewed as a forerunner of expeditions to come. Many disciplines relevant to the unique biology of the central Pacific were not represented in 1988, particularly those concerned with the functioning of coral reef ecosystems. Steps have been taken to issue a broader call to marine biologists to participate in future expeditions in order to further our understanding of the World Ocean and the marine-derived shallow waters and terrestrial ecosystems of which it is composed. If the publication of this volume inspires other biologists to follow, it has fulfilled part of its goal in presenting the varied findings of a successful initial expedition.

Appendix A

Participants of the First Joint US–USSR Pacific Expedition, Fall 1988.

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